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THE INHERITANCE OF HULL–LESSNESS IN OAT HYBRIDS[1]

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THE purpose of this paper is to set forth some results obtained in certain crosses between the hull-less types of oats and some of the hulled forms.

The hull-less types belong to the species *Avena nuda*. The origin of these forms is not definitely known, although, according to Carleton,[2] they appear to have come from central and eastern Asia. Reports are to the effect that a certain form of this oat has been cultivated in China for a thousand years or longer. These types are not generally cultivated in any other countries and perhaps due to this fact little study has been made of the various hull-less types and their possible origin. From some observations made on our material it seems quite possible that these hull-less forms may have originated through mutative changes. For example, in a pure line of the variety Sixty Day certain spikelets suddenly appeared which were very similar to the true hull-less forms in having the caryopsis loosely held in the glumes and an increased number of flowers per spikelet. These seeds were tested, but did not reproduce this hull-less tendency. A large number of similar cases have been observed particularly with hybrids, although none of these

[1] Paper No. 68, Department of Plant Breeding, Cornell University, Ithaca, N. Y.

[2] "The Small Grains," 1916.

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has been tested as to its inheritance as yet, but it is planned to do so.

Trabut[3] says in regard to the possible origin of hull-less oats that ''the study of the domestication of Avena presents, from the genetic point of view, some rather substantial arguments in favor of an ambient medium, a modifying agent causing fluctuations which end in the formation of varieties well characterized and fixed by selection.''

Previous Work

A number of investigators have studied hybrids between varieties of *Avena nuda* and *Avena sativa*. Norton[4] was the first investigator in America to hybridize these forms. He reports that

the spikelet of the naked varieties usually has more than three grains, while in the hulled types three grains is the limit. The first generation plants produced a head naked at the top and hulled at the bottom. In the second generation, one fourth of the progeny were typical naked plants, one fourth were hulled, and one half like the first generation hybrids. The naked plants all had long spikelets with more than three grains, while the hulled plants had spikelets with the usual two or three grains. In future generations no exception to this rule has been found except that one second generation plant of a cross between European Hull-less and Garton's Tartar King which seems to have become fixed in the intermediate hybrid type. In this example we have an extremely rare case of the fixation of a heterozygote or hybrid type.

Gaines[5] reports having made some hybrids between hulled and hull-less oats and first separated the F_2 types into two groups, hulled and hull-less. In making such a grouping the heterozygous types were put into the group which it resembled most. He obtained from one cross 48.7 per cent. hulled and 51.3 per cent. hull-less plants and says, ''this indicates an intermediate about half-way between hulled and hull-less for the heterozygous types. As was mentioned above, the separation was made arbitrarily into hulled and hull-less, according to the type any given plant most nearly resembled.''

[3] *Journal of Heredity*, Vol. 5, p. 84, 1914. Translation of original paper.
[4] American Breeders' Association, Vol. III, p. 285, 1907.
[5] Washington Agr. Expt. Sta. Bul. 135, p. 58, 1917.

In another çross Gaines found 77.1 per cent. hulled to 22.9 per cent. hull-less, which caused him to conclude that the two crosses were not similar in their behavior. This would seem to be the case from the data at hand, yet in 1914 Gaines made a number of other crosses, among which according to the pedigree numbers is another one between these two sorts, Black (Wash. No. 665) and Hulless (Wash. No. 680) which gave, this time, results very similar to all the other crosses reported as made that year, which indicated a $1:2:1$ ratio. Gaines did not offer any explanation as to the different behavior of these two crosses between the same two sorts.

From these experiments Gaines concludes,

the percentage of hulled type suggests a simple Mendelian recessive although in every case there are a few too many hulled plants. The percentage of hull-less plants is not only very irregular in the different crosses but is also irregular in the different families within the same cross with the exception of the two families of Sixty Day $\times$ Hull-less, which gave a ratio approaching $1:2:1$. The intermediate types showed great variation. Plants could be found with only one or two spikelets that showed the hull-less character. Others could be found that showed the hulled character in only one or two spikelets, and plants were obtained with every degree of hull-lessness between these extremes. However, most of the intermediates produced more than half hulled oats. A curve fitted to these intermediate variations in Black Tartarian $\times$ Hull-less shows larger numbers at either extreme and few numbers showing per cents. of hulled oats ranging from 30 to 50. This is just the opposite of what we would expect if the hull-less character was caused by a single Mendelian unit which produced an intermediate in the F_1.

In a paper by Zinn and Surface[6] results are given of a cross between a hull-less and hulled oat. The sorts used were *Avena sativa patula* var. Victor, and *Avena sativa nuda* var. *inermis*. The results indicate that their forms agree very closely with those reported by Norton and Gaines. The following paragraph gives part of their conclusions.

The F_1 generation is distinctly intermediate in most characters. In regard to the glumes, both naked and firmly hulled grain as well as intermediate forms are found on the same panicle and even in the same

spikelet. As shown in Table I, the spikelets near the top of the panicle are either entirely naked or nearly so, while those spikelets near the base of the panicle tend to be firmly hulled. A similar but less marked relation is to be observed between the spikelets at the tip and base of each whorl.

In the F_2 generation a large number of intermediate forms appear. In addition to the two parental hull types, four intermediate classes were distinguished. These intermediate forms contain all gradations from the plants with perfectly hulled grain to the perfectly naked forms.

As shown in Table II, the inheritance of the hull characters presents a simple Mendelian relation giving 1 hulled, 2 intermediate, 1 naked. Likewise, in respect to grain color, there are 3 black plants to 1 white, in the second generation.

Material and Methods

In connection with some experiments in oat breeding a number of hybrids between the hulled and hull-less forms have been made. While in these crosses the inheritance of other characters such as color of glumes, pubescence, awns and the like, are very interesting, the present paper will be confined to the discussion of the inheritance of the hull-less and hulled characteristics. A more complete discussion of the various characters is being prepared for a later publication.

The authors want to take this opportunity to express their appreciation for the valuable assistance in note-taking and tabulation of results rendered by W. T. Craig and Miss A. M. Atwater. Their work has been of great aid in conducting these experiments.

The hull-less oat used for the various hybrids was typical of the *Avena nuda* group and differs from the *Avena sativa* forms by three important characters: (1) The lemma, or flowering glume, and palet do not clasp the kernel as in other forms, and the kernel is therefore loose, or free, within the hull; (2) The rachillæ of the three to many-grained spikelet are so elongated that the uppermost grains are borne above the empty glumes; (3) The glumes and the lemmas are similar in texture. The illustration (Fig. 1) will give a fair idea of the par-

Fig. 1. The Female Parent (*Avena nuda*) Used in Series 382.

ticular characteristics which separate *Avena nuda* from the hulled species.   This type is typical of the hull-less forms used in the following hybrids.

The hulled forms were all varieties of *Avena sativa* with one exception.   In this case *Avena fatua* was used

Pure hulled spikelet

FIG. 2. THE MALE PARENT (*Avena sativa*) USED IN SERIES 382.

as the hulled parent. Fig. 2 shows the hulled variety, Sixty Day, used in one of the crosses. It is typical of a hulled oat.

The first crosses of this sort were made in 1910 and the F_1 plants grown in the greenhouse the following winter. The first cross was between Hulless and Black Tar-

tarian. Here the hull-less form was used as the female parent. The male parent possessed, as indicated by its name, black glumes, and was a typical hulled oat. The other cross was between Danish Island and Hulless in which the hulled type was used as the female parent. In each case the F_1 type was typical of the F_1 types as described by the authors mentioned above. This form is intermediate in that both kinds of kernels, hulled and hull-less, are found on the same head. The type of panicle resembles the hull-less parent more than it does the hulled and may be considered as intermediate in type. There are some spikelets with hulled and some with hull-less kernels and also some with both hulled and hull-less kernels. As a usual thing the hulled spikelets occur towards the base of the panicle while the hull-less kernels occur near the terminal spikelet which is almost invariably hull-less if such kernels are present at all in the panicle.

There are fewer hulled than hull-less kernels on the F_1 types. The percentage of hulled kernels does not usually run very high. In Fig. 3 is shown a typical form of F_1 panicle of a cross between a hulled and hull-less oat.

The F_2 generation of these two crosses were grown in the field in the summer of 1913. The plants were then sorted into two groups, hulled and hull-less, or hull-less like. All those plants having any indication of hull-lessness were placed in the hull-less class. The result of these counts was as follows:

Series Number	Varieties Crossed	Hull-less	Hulled
111	Hulless × Black Tartarian....................	129	37
51	Danish Island × Hulless.....................	364	93
		493	130

Although the ratio deviates considerably from 3:1 it indicates that this character behaves as a simple monohybrid and that there is one factor pair concerned. In
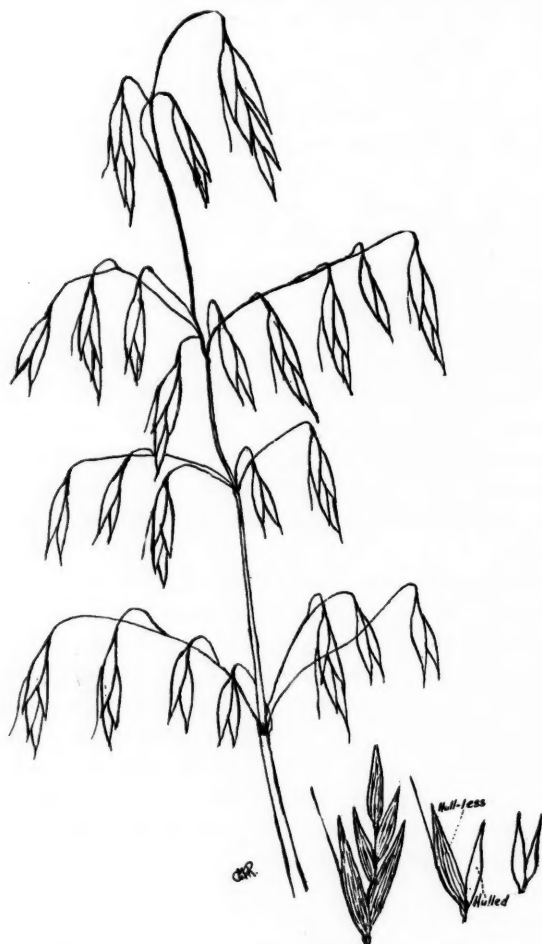
Fig. 3.   F₁ Intermediate Type of a Cross Between Hull-less and Hulled.
Series 382.

order to test this out more fully all plants from which
good seed could be obtained were grown in the following
year.   The results obtained from these plants showed
without doubt that the segregation followed a simple
monohybrid ratio.   That is, the pure hulled and hull-less
plants bred true to these characteristics, while the inter-

mediate types reproduced the three types again. The
second generation plants tested as to their composition
gave the following results in the third generation:

Series Number	Varieties Crossed	Pure Hulled	Inter-mediate	Pure Hull-less
111	Hulless × Black Tartarian	37	85	38
51	Danish Island × Hulless	115	216	114
		152	301	152

It is apparent from these results that certain plants were
classed as intermediate in the second generation, which
were in reality pure hulled plants. It is evident that the
hulled-hull-less character is inherited in a simple Men-
delian fashion so far as its general behavior is con-
sidered.

The heterozygous plants produced in the third gen-
eration were examined as to the relative amounts of
hulled and hull-less kernels present. This was done by
threshing a representative head from each plant by hand
and counting the hulled and naked kernels and express-
ing the result as the percentage of hulled kernels.

In order to determine whether the results from a
single head fairly represented the type of the plant a
number of plants were examined and recorded a head at
a time. The percentage of hulled kernels for a represen-
tative head was then compared with that for the entire
plant. The average percentage was the same for the
results from single heads as it was for the entire plant.
Although there was some deviation in the individual de-
terminations, the correlation between the two methods is
very high.

The result of determining the percentage of hulled
kernels was to indicate the great variation existing,
which was from a very low to a very high percentage.
As a result of these observations it was apparent that
while in the hybrids under consideration the usual $1:2:1$
ratio was observed, some factor or factors were pres-

ent which affected the heterozygous forms in such a way as to modify the amount of hulled or hull-less kernels present.

In order to determine this effect in a more definite way it was planned to sow seed from heterozygous individuals which differed as to the percentage of hulled kernels present. A rather large number of such seeds were planted in 1915. The plants were severely injured by a storm, so that accurate percentage determinations could not be made.

In the meantime, however, a number of other crosses had been made in which the *Avena nuda* was used as one parent. The following sorts were crossed with the naked oats: Swedish Select, Sixty Day and *Avena fatua*. Other crosses are being studied but these will be reported on later.

As regards the hull-less character the F_1 individuals of these crosses were all similar to the description of the first generation given earlier in this paper. Regarding the other characters, the cross between the hull-less form and *Avena fatua* showed some very interesting variations. These will not now be discussed.

Seeds of these various F_1 plants were sown and the resulting plants harvested. From each plant a head was saved and threshed separately by hand and the plants then sorted into hulled, intermediate and hull-less. The result of the several crosses is given here:

Series Number.	Varieties Crossed	Hulled	Intermediate	Hull-less
379	Hulless × *Avena fatua*	68	111	78
202	Hulless × Swedish Select	41	90	36
382	Hulless × Sixty Day	75	193	53
	Observed	184	394	168
	Expected	186.5	373	186.5

The probable error is ± 7.98 and the observed numbers agree fairly well with the expected numbers. The number of hull-less plants is too low and the number of intermediates too high. It is possible that in some cases
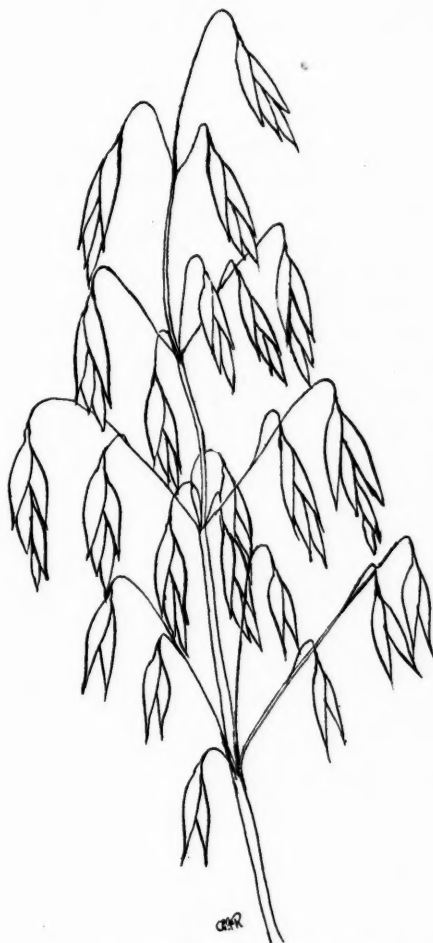
FIG. 4. HETEROZYGOUS TYPE F_4 POSSESSING 10 PER CENT. OF HULLED KERNELS.
Series 382.

hull-less plants may have been recorded as intermediates although the error from this source is not large.   When the results are considered on a 1 : 3 basis and the hull-less and intermediates are grouped together we find that there is a percentage of 24.66 ± 1.07 hulled plants.
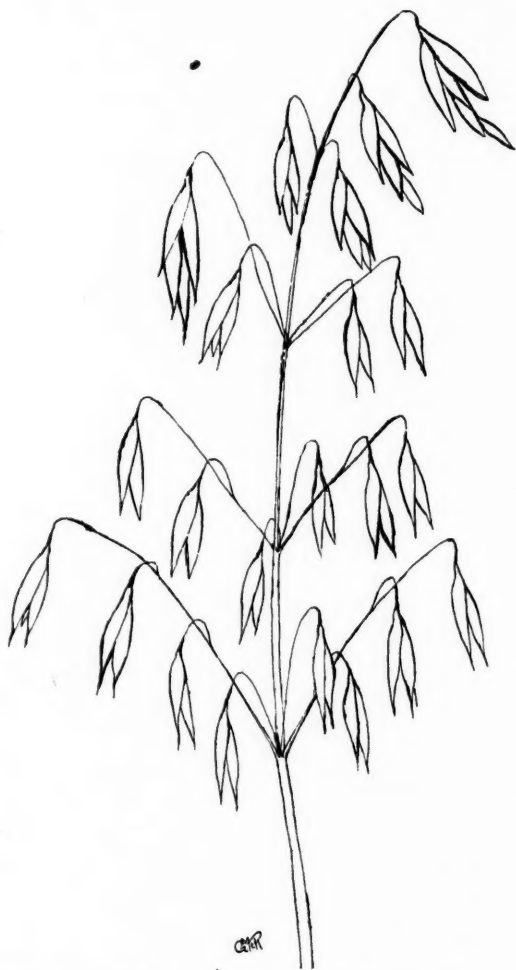
FIG. 5.   HETEROZYGOUS TYPE F₄ POSSESSING 87.9 PER CENT. OF HULLED KERNELS.
Series 382.

The results of these different hybrids show that hull-lessness is inherited in a simple monohybrid manner and that without doubt the difference between hulled and hull-less oats in this regard is represented by one pair

of factors. An analysis of the different heterozygous or intermediate individuals of these second generation plants showed that for these hybrids also there was a great amount of variation in the percentage of hulled or hull-less kernels in the individual plants, the variation ranging all the way from less than 5 per cent. to 95 per cent. or more. In Figs. 4 and 5 are shown two forms of heterozygous plants, one very low and one very high, in percentage of hulled kernels. These percentages were obtained from the heterozygous individuals by sorting the kernels from one head of each plant into hulled and hull-less as outlined earlier. The percentage of hulled kernels on the heterozygous plants of the second generation for the three series is given in Table I.

TABLE I

SHOWING PERCENTAGE OF HULLED KERNELS ON THE HETEROZYGOUS PLANTS
OF THE SECOND GENERATION IN CROSSES BETWEEN HULLED
AND HULL-LESS OATS.

Series Number	Varieties Crossed	Percentage of Hulled																			
		2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5	87.5	92.5	97.5
379	Hulless × *Avena fatua*		2	3	5	4	4	3	4	4	7	5	5	8	4	6	5	7	10	13	15
202	Hulless × Swedish Select	10	4	4	3	5	8	2	1	7	6	3	4	2	5	3	3	6	3	4	6
382	Hulless × Sixty Day	5	5	5	4	4	6	6	8	20	15	22	21	15	13	17	11	7	4	4	1
		15	11	12	12	13	18	11	13	31	28	30	30	25	22	26	19	20	17	21	22

From this table it is seen that there is considerable difference in the percentage of hulled kernels on the different heterozygous plant. The range is from a very low percentage or one which indicates nearly all hull-less to a very high percentage or one which is nearly all hulled. There is no general grouping near the middle of the series, as might be expected with the exception of series 382. This may be due to lack of numbers or to a segregation of the different types which give percentages ranging from low to high without any tendency to grouping. That it is not due to lack of numbers is probably

borne out by the fact that in series 51, where over 900 plants of the third generation were sorted into the different classes, there was no indication of a grouping near the middle classes, in fact, the slight indication of grouping was near the lower values. The distribution is as follows:

TABLE II

SHOWING PERCENTAGE OF HULLED KERNELS IN THE HETEROZYGOUS PLANTS OF THE THIRD GENERATION IN A CROSS BETWEEN DANISH ISLAND AND A HULL-LESS OAT.

Percentage of Hulled Kernels	Frequency	Percentage of Hulled Kernels	Frequency
0 − 4.9	89	50.0 −54.9	42
5.0 − 9.9	80	55.0 −59.9	48
10.0 −14.9	60	60.0 −64.9	43
15.0 −19.9	49	65.0 −69.9	26
20.0 −24.9	59	70.0 −74.9	35
25.0 −29.9	48	75.0 −79.9	33
30.0 −34.9	47	80.0 −84.9	32
35.0 −39.9	53	85.0 −89.9	26
40.0 −44.9	52	90.0 −94.9	21
45.0 −49.9	46	95.0 −99.9	15

It was planned to carry some of this work further to answer in general two questions which are: (1) Does the percentage of hulled plants obtained from any heterozygous parent vary with the percentage of hulled kernels possessed by that parent? (2) Do the hulled and hull-less kernels of a heterozygous plant give approximately the same results in their offspring?

In order to obtain data on these questions two of the series have been continued. The hull-less-*Avena fatua* series has not been carried further as yet but it is planned to do so.

RESULTS FROM SERIES 202—SWEDISH SELECT × HULLESS

The first series to be discussed is the Swedish Select-Hull-less cross. Seed from two hulled and two hull-less plants of the second generation were grown in the third generation and each bred true to type. In addition to these plants twenty heterozygous plants were selected for planting. These varied as to the amount of hulled

kernels. The range was from 3.2 per cent. to 92.0 per cent. The number of seed was not large, therefore the number of plants obtained was not as large as desired, yet from the consistency of the results certain conclusions are justified. The offspring from these twenty plants were sorted into the three classes, hulled, intermediate and hull-less. The intermediate plants were again threshed and the percentage of hulled kernels determined.

In Table III is given the percentage of hulled condition in the parent plant, the segregation into the three groups, the percentage of hulled kernels in the heterozygous offspring, the grouping into hulled and hull-less and (where both hull-less and intermediate plants are grouped together) the percentage of hulled plants with the probable error.

TABLE III

SHOWING SEGREGATION IN F_3 OF CERTAIN F_2 PLANTS TOGETHER WITH THE PERCENTAGE OF HULLED SEED IN PARENT TYPE AND THE AVERAGE PERCENTAGE IN THE HETEROZYGOUS OFFSPRING.

	Segregation Obtained from Plants Sown and Resulting Percentage of Hulled Kernels on Intermediate Forms.							
	Per Cent. of Hulled Kernels in Plants Sown	Hulled	Intermediate	Hull-less	Per Cent. Hulled in Intermediate Offspring	Hulled	Hull-less and Intermediate	Per Cent. Hulled and P. E.
202a1–4...	44.9	27	63	22	44.8	27	85	24.11 ± 2.76
6...	25.0	34	51	40	21.0	34	91	27.20 ± 2.61
9...	20.9	27	35	60	12.8	27	95	22.13 ± 2.64
10...	83.0	42	63	34	39.5	42	97	30.22 ± 2.48
11...	92.0	42	62	17	52.6	42	79	34.71 ± 2.65
22...	65.1	13	36	7	60.6	13	43	23.21 ± 3.90
25...	90.3	14	36	9	55.3	14	45	23.73 ± 3.80
26...	76.6	14	37	21	56.3	14	58	19.44 ± 3.44
29...	30.7	12	19	15	44.1	12	34	26.09 ± 4.31
31...	56.8	16	43	21	47.6	16	64	20.00 ± 3.27
38...	10.5	21	26	40	22.3	21	66	24.14 ± 3.13
40...	82.4	19	33	19	53.6	19	52	26.76 ± 3.47
46...	16.7	14	20	22	24.7	14	42	25.00 ± 3.90
51...	56.6	25	41	10	47.1	25	51	32.89 ± 3.35
60...	74.3	7	10	4	46.0	7	14	33.33 ± 6.37
66...	3.2	10	26	32	22.7	10	58	14.71 ± 3.54
77...	65.4	15	21	14	34.9	15	35	30.00 ± 4.13
92...	35.3	12	10	8	36.0	12	18	40.00 ± 5.33
120...	44.7	14	18	8	33.9	14	26	35.00 ± 4.62
121...	9.5	13	11	23	20.2	13	34	27.66 ± 4.26
Totals......		391	661	426		391	1087	26.45 ± .76
Expected....		369.5	739	369.5				

The results of the segregation into the three classes gave 391 hulled, 661 intermediate and 426 hull-less. Here the hull-less plants are too great in number, while the number in the intermediate class is too small. The expected numbers are $369.5 : 739 : 369.5$, with a probable error of ± 11.23. It is possible that some intermediate plants were classed as hull-less. Such a condition is possible since some intermediates are found bearing only one or two hulled kernels, and if these should be lost through shattering, such plants would be classed as hull-less when in reality they are intermediates. When the grouping is made into the two groups, hulled and hull-less, it is seen that the 3 to 1 ratio is approximated very closely, as there are 391 hulled plants to 1087 hull-less, giving a percentage of $26.45 \pm .76$ hulled.

An examination of this table shows further that some of the families do not give ratios close to $1 : 2 : 1$. This is true with regard to certain families particularly with certain of those coming from plants low in percentage of hulled, and some of those relatively high in this respect. The results of some of these families have been brought together in Table IV.

TABLE IV

Showing Segregation of Offspring Coming from Some Individuals Low or High in the Percentage of Hulled Kernels.

Family Number	Percentage of Hulled Seed in Plants Sown	Segregation of Offspring Into Different Types.		
		Hulled	Intermediate	Hull-less
6	25.	34	51	40
9	20.9	27	35	60
38	10.5	21	26	40
46	16.7	14	20	22
66	3.2	10	26	32
121	9.5	13	11	23
	Total.........	119	169	217
10	83.	42	63	34
11	92.	42	62	17
25	90.3	14	36	9
26	76.6	14	37	21
40	82.4	19	33	19
	Total.........	131	231	100

In this table the plants from parents having 25 or less per cent. of hulled kernels give 119 hulled : 169 intermediate : 217 hull-less. From this result it appears that those plants having a low percentage of hulled or high percentage of hull-less kernels tend to produce a relatively high number of hull-less plants. On the other hand, those plants having more than 75 per cent. of hulled kernels do not give results so striking. There are more hulled than hull-less plants, yet not strikingly so, and the hulled do not run higher than the intermediates. It may be, however, that the degree of hull-lessness as expressed by the percentage may influence the segregation in the following generations. This can not be definitely stated from this cross, and further evidence will be needed.

TABLE V

SHOWING THE RELATION BETWEEN THE PERCENTAGE OF HULLED KERNELS ON THE HETEROZYGOUS PARENT PLANTS AND THE PERCENTAGE OF HULLED KERNELS ON ITS OFFSPRING

Percentage of Hulled Oats on Plants Sown	Percentage of Hulled Oats on Offspring																				
	0-4.9	5.0-9.9	10.0-14.9	15.0-19.9	20.0-24.9	25.0-29.9	30.0-34.9	3.50-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9	70.0-74.9	75.0-79.9	80.0-84.9	85.0-89.9	90.0-94.9	95.0-99.9	
3.2	12	3		3	1	1				1		1			1	1		1	1		26
9.5	1	1	2	2	2	1			1	1											11
10.5		5	2	3	6	6	1	1	1		1										26
16.7	2	3		3	4	2	1	2		2					1						20
20.9	9	10	7	4		1	2			1	1										35
25.0	5	12	4	6	5	2	9	2	4	1		1									51
30.7	1	1		1		1	2	2	2	2	1	1	1	1	2	1					19
35.3		2		1	1	1	1	1	1						1				1		10
44.7	1	1	1		2	4	3			3	2	1									18
44.9	4	3	6		3	1	6	3	2	3	4	7	7	6	0	6	2				63
56.6	1	3	1	1	3		3	2	6	3	3	2	3	3	1	2	2	1		1	41
56.8			5	1	1		4	3	2	2	4	2	5	6	2		3	2	1		43
65.1	2	3									6	4	2	4	2	6	4	1	2		36
65.4	1	5	1	1	1	4			2	1		1		1				1	1	1	21
74.3	1	1		1			1			1	1		1	1				1	1		10
76.6				1	2	3	2	1	1	1	3	4	5	1	1	1	6	4		1	37
82.4				1	1	2		2	3	3	4	3	3	1	1	2	2	2	1	2	33
83.0	5	1	2	8	4	5	2	7	5	2	5	3	3	5	2	1	2			1	63
90.3	4	2	2		1				3		3	1	7	1	5	3	3	1			36
92.0	1	4	2	1	3	3	2	3	2	5	5	6	4	2	4	4	7	1	3		62
	50	60	37	39	41	39	39	30	32	36	39	42	32	34	18	32	32	15	12	2	661

The relation between the percentage of hulled kernels on the parent and the percentage of hulled kernels on the heterozygous offspring for this series is shown by the correlation table given above. The correlation coefficient is. $421 \pm .022$, which shows a very definite relation between the percentage of hulled in the parent and offspring.

This relation is also better shown by means of a curve (Fig. 6) in which the parents are represented by the dotted line beginning with the lowest and increasing to the highest value. On the same ordinate is plotted the average value for the heterozygous offspring, and to this line has been fitted a straight line whose equation is $y = 20.1999 + 1.9579x$.

Certain of these families show a decided grouping; for example that represented by 20.9 per cent. shows a decided tendency to be grouped in the lower classes, while that represented by 65.1 per cent., with five exceptions, shows a grouping around the higher classes.

Results of Series 382—Sixty Day × Hull-less

From the second generation of this cross six heterozygous plants were selected for further study. The results of three of these will be discussed here. These plants possessed different amounts of hulled kernels, which expressed in percentages were as follows, 73.3, 37.7, 49.3. Thus, there was one high, one low and one medium plant. The offspring of these gave the following results when grouped in the three classes:

	Hulled	Intermediate	Hull-less
382a1–7....	23	55	20
8.....	15	37	24
9.....	53	105	49
	91	197	93

These figures agree very well with the expected $1:2:1$ ratio. Single heads of the heterozygous plants of these three families were threshed and the percentage of hulled

kernels per plant determined as before.   The three fam-
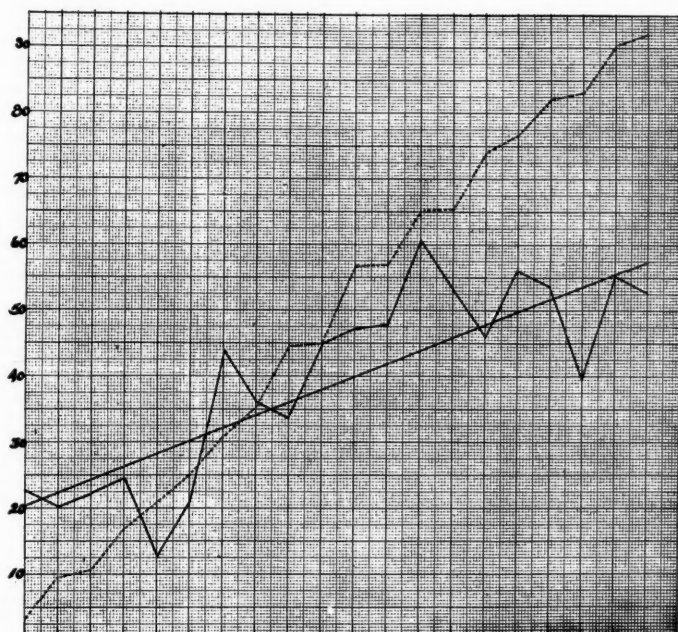ilies gave the following distribution:

FIG. 6.   These curves show the relation between the percentage of hulled
grain on the heterozygous plant used as parent and the average percentage of
hulled kernels on its heterozygous offspring.   Dotted line represents the value
for the parents and the solid line that of the heterozygous offspring.   Series 202.

From these distributions it is clear that the percentage
of hulled kernels on the parent form influences the
amount of the hulled condition.   The average percentage
of the offspring in each case agrees closely with that of
the parent forms.

From these three families several plants differing in
their percentage values were selected to continue the
study in the fourth generation.   As observed from the
frequency distribution just given it is noted that series
7 is of high value, while 8 is relatively low and 9 varies
from very low to high.   The plants selected then in gen-

eral represented the types of their lines; that is, those from 7 were generally high, those from 8 generally low, and those from 9 both low and high. The offspring of these various selections are arranged in a table similar to that for series 202.

Series No.	Percentage Hulled Seed in Plant Sown	0-4.9	5.0-9.9	10.0-14.9	15.0-19.9	20.0-24.9	25.0-29.9	30.0-34.9	35.0-39.9	40.0-44.9	45.0-49.9	50.0-54.9	55.0-59.9	60.0-64.9	65.0-69.9	70.0-74.9	75.0-79.9	80.0-84.9	85.0-89.9	90.0-94.9	95.0-99.9	Totals	Average Per Cent of Hulled Kernels on Offspring
						Percentage of Hulled in Offspring																	
382al-7	73.3					1				1	3	5	5	5	6	12	10	6	1			55	67.3
8	37.7	1	1	2	3	3	6	4	5	2	5	2	1	2									37	33.7
9	49.3	1	1	3	6	7	6	5	4	4	14	5	8	11	11	7	8	1	1	2			105	50.1
		2	2	5	9	11	12	9	9	7	22	12	14	18	17	19	18	7	2	2				

TABLE VI

SHOWING SEGREGATION IN F_4 OF CERTAIN F_3 PLANTS TOGETHER WITH THE PERCENTAGE OF HULLED SEED IN PARENT TYPE AND THE AVERAGE PERCENTAGE IN THE HETEROZYGOUS OFFSPRING

	Per Cent of Hulled Kernels in Plants Sown	Hulled	Intermediate	Hulless	Per Cent Hulled in Intermediate Offspring	Hulled	Hulless and Intermediate	Per Cent Hulled and P. E.
	Segregation Obtained from Plants Sown and Resulting Percentage of Hulled Kernels on Intermediate Forms.							
382al-7-10..	63.6	22	31	25	63.1	22	56	28.21 ± 3.31
11..	53.0	24	34	10	46.0	24	44	35.29 ± 3.54
32..	77.0	28	38	22	70.5	28	60	31.82 ± 3.11
33..	70.3	21	53	26	62.7	21	79	21.00 ± 2.92
37..	80.0	8	31	19	57.5	8	50	13.79 ± 3.84
45..	81.7	13	27	13	75.1	13	40	24.53 ± 4.01
55..	63.0	19	39	28	67.8	19	67	22.09 ± 3.15
8-14..	43.6	26	34	19	37.6	26	53	32.91 ± 3.29
17..	38.2	28	63	23	44.1	28	86	24.56 ± 2.74
22..	23.2	15	36	14	25.3	15	50	23.08 ± 3.62
23..	17.0	4	9	9	19.2	4	18	18.18 ± 6.23
28..	60.8	12	30	13	49.8	12	43	21.82 ± 3.94
35..	17.2	22	43	24	20.5	22	67	24.72 ± 3.10
61..	59.6	13	27	11	50.6	13	38	25.49 ± 4.09
64..	9.8	16	36	14	25.3	16	50	24.24 ± 3.60
9- 9..	14.0	4	29	7	19.2	4	36	10.00 ± 4.62
44..	62.4	24	50	15	49.1	24	65	26.97 ± 3.10
94..	23.6	15	21	20	22.2	15	41	26.79 ± 3.90
166..	79.7	16	27	22	81.2	16	49	24.62 ± 3.62
175..	87.9	19	32	17	67.2	19	49	27.94 ± 3.54
Totals		349	690	351		349	1041	25.11 ± .78
Expected ...		347.5	695	347.5		347.5	1042.5	

The total number of plants in the hulled, intermediate and hull-less classes agree very closely with the expected numbers. The same is true for the $3:1$ grouping, since the percentage of hulled is $25.11 \pm .78$, which shows without doubt that the various families give offspring which follow the $1:2:1$ expectancy.

In this series there is little evidence that the percentage condition of the parent plant affects the type of segregation in the following generation. In general the segregation of the various families follows a $1:2:1$ ratio regardless of the percentage condition of the parent.

To show the relation between the hulled condition of the parent forms and that of the heterozygous offspring a correlation table was made in which the different families were arranged according to their percentage values. The coefficient of correlation here is $.726 \pm .012$, which

TABLE VII

SHOWING THE RELATION BETWEEN THE PERCENTAGE OF HULLED KERNELS ON THE HETEROZYGOUS PARENT PLANTS AND THE PERCENTAGE OF HULLED KERNELS ON ITS OFFSPRING

Percentage of Hulled Oats on Plants Sown	Percentage of Hulled Oats on Offspring																				Total
	0–4.9	5.0–9.9	10.0–14.9	15.0–19.9	20.0–24.9	25.0–29.9	30.0–34.9	35.0–39.9	40.0–44.9	45.0–49.9	50.0–54.9	55.0–59.9	60.0–64.9	65.0–69.9	70.0–74.9	75.0–79.9	80.0–84.9	85.0–89.9	90.0–94.9	95.0–99.9	
9.8	2	2	4	5	4	5	7	2	3	2											36
14.0	2	7	7	3	1	2	2	1	2	2											29
17.0	1		2	1	3	1	1														9
17.2	2	7	6	11	4	5	3	1	3					1							43
23.2	2	2	4	5	4	7	2	3	2												36
23.6	2			6	7	2	1	1			1										20
38.2						2	3	12	11	11	8	7	3	1	3				2		63
43.6			2		5	2	4	5	6	6	1	2	1								34
53.0		1	1	2	1	3		2	2	6	5	6	1	2	1	1					34
59.6						1		4	2	4	8	4	2	1	1						27
60.8				1		2	1	3	4	3	6	2	3	3	2						30
62.4	4	2	2	1		1	4	2	3	5	9	6	4	4	1			2			50
63.0	1					2			1	2	5	1	6	5	8	5	1	2			39
63.6				1			2	1	1	2	2	2	1	9	1	2	6	1			31
70.3							1	1	2	2		7	9	7	9	5	6	1	3		53
77.0			1				1			1		4	1	5	9	6	5	3	1		37
79.7							1		1	1		2	1	4	4	1		10	2		27
80.0	1	1				3			1	3	4	1	3	6	2	3	1	1		1	31
81.7											1		3	3	5	8	3	3	1		27
87.9				1				1		2	4	2	4	3	2	2	5	4	1		31
	17	22	29	37	31	35	45	41	42	46	54	49	34	57	38	40	31	17	17	5	687

is considerably higher than it was with the 202 series. One reason for this may be that perhaps there is a difference between this series and the former or that the result is caused by grouping the three families. When a correlation table is made for each of the three families
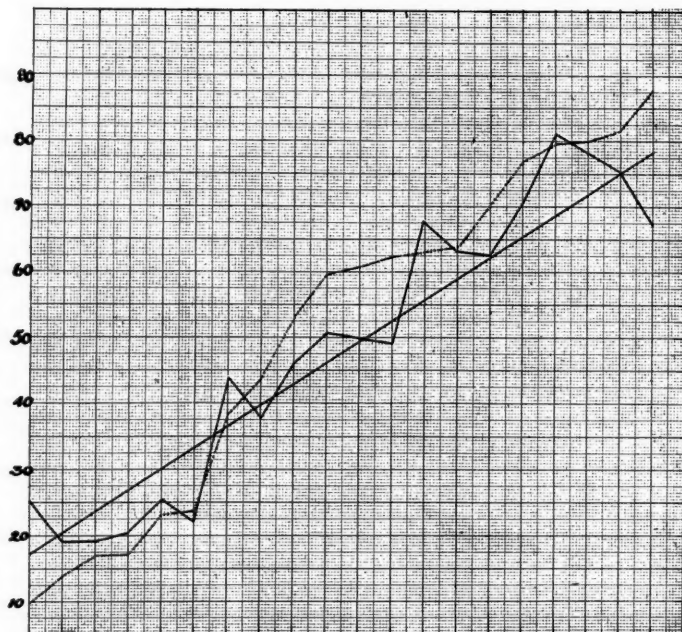

FIG. 7. These curves show the relation between the percentage of hulled grain on the heterozygous plant used as parent and the average percentage of hulled kernels on its heterozygous offspring. Dotted line represents the value for the parents and the solid line that of the hetrozygous offspring. Series 382.

separately, correlation coefficients of .296 $\pm$ .039, .623 $\pm$ .025 and .741 $\pm$ .024 are obtained. Thus it is seen that within any family correlation exists to a greater or less degree. Putting the three families in one table does increase the correlation somewhat over the average value for each alone. Another and possibly more plausible reason is the fact that these plants are of the fourth generation, while those of 202 are of the third.

The three parent series from which these were taken were of three types as mentioned before, therefore the parent plants selected from them carried the tendency to produce high or low as the case may be, and when they are all arranged in a correlation table naturally a high coefficient is obtained. In other words, the three parent forms were more nearly homozygous, so to speak, for high or low values. More will be said on this point later.

This relationship was further shown by means of a graph showing the relation between the parent percentage condition and the average value for the offspring, the same as was done in Fig. 7.

In this case the relationship is higher than in the former series. The equation to the straight line is $y = 17.2411 + 3.2062x$.

That the plants arising from heterozygous plants having a low or high percentage of hulled kernels did not segregate in a manner indicating any influence of the hulled condition of the parent plant, as was the case to some extent with series 202, is shown in Table VIII.

TABLE VIII

Segregation Obtained when Sowing Seed from Heterozygous Plants Having Low or High Percentages of Hulled Seed

Percentage of Hulled Kernels in Plants Sown	Segregation of Offspring Into Different Types		
	Hulled	Intermediate	Hull-less
9.8	16	34	14
14.0	4	29	7
17.0	4	9	9
17.2	22	43	24
23.2	15	36	14
23.6	15	21	20
	76	172	88
77.0	28	38	22
79.7	16	27	22
80.0	8	31	19
81.7	13	27	13
87.9	19	32	17
	84	155	93

It is clear that the percentage of hulled seeds does not seem to influence the segregation as far as these data are concerned.

Hulled Compared with Hull-less Kernels

In order to learn whether there was any difference in the ratios produced by the hull-less kernels from the heterozygous plants the seed from the third generation plants used was separated and planted separately; that is, the hulled and hull-less from family 382a1–7–45 was planted separately so that the ratio may be determined on each lot of plants. This was done for all the families. These results are given in Table IX.

TABLE IX

RESULTS OBTAINED FROM SOWING HULLED AND HULL-LESS SEED FROM THE SAME HETEROZYGOUS INDIVIDUAL SEPARATELY

Family No.	Segregation Obtained from Hulled Seeds			Segregation Obtained from Hull-less Seeds		
	Hulled Plants	Intermediate Plants	Hull-less Plants	Hulled Plants	Intermediate Plants	Hull-less Plants
382a1–7– 45......	11	26	12	2	1	1
7– 10......	18	22	20	4	9	5
7– 11......	19	27	10	5	7	0
7– 32......	18	28	17	10	10	5
7– 33......	20	39	21	1	14	5
7– 37......	8	25	19	0	6	0
7– 55......	14	31	25	5	8	3
8– 14......	18	19	8	8	15	11
8– 17......	10	28	12	18	35	11
8– 22......	3	7	4	12	29	10
8– 23......	4	6	6	0	3	3
8– 28......	9	18	8	3	12	5
8– 35......	5	16	7	17	27	17
8– 61......	9	19	9	4	8	2
8– 64......	3	7	4	13	29	10
9– 9......	3	6	3	1	23	4
9– 44......	16	35	13	8	15	2
9– 94......	7	8	7	8	13	13
9–166......	13	22	14	3	5	8
9–175......	19	30	16	0	2	1
Totals.............	227	419	235	122	271	116
Expected Nos.......	220.25	440.5	220.25	127.25	254.5	127.25

In many of the cases the numbers are too small to give good ratios, yet the important point is obtained from the summation of the two series. In each case these agree very closely with the expected numbers. If there was any difference we might expect the hulled kernels to produce relatively more hulled plants and the hull-less rela-

tively more hull-less. The facts are the reverse. In the series from the hulled kernels the hull-less plants are in the majority and the opposite is true for the hulled plants from the hull-less seed. It is very evident that there is no relation between the kind of kernel (hulled or hull-less) sown from a heterozygous plant and the off-spring produced.

General Discussion

From the foregoing data it seems without doubt that the inheritance of the hulled condition follows a simple Mendelian ratio giving in general 1 hulled, 2 inter-mediate, 1 hull-less. This is in accord with the results obtained by Norton, Gaines, Zinn and Surface, and others.

In regard to the relation between the hulled condition of the heterozygous parent plants and of the offspring, it is clear that there is a very close agreement in regard to the hulled percentage. When high or low plants are selected they produce heterozygous offspring giving high or low percentage. In most cases, however, the usual 1:2:1 ratio is obtained. This is true in general in all cases of the 382 series but not so for 202. Whether the 202 series behaves differently or whether in reality it will agree with 382 will have to be determined with further work.

The percentage relation shows that there is a variation from very low to a very high percentage. Owing to this fact and that any heterozygous plant tends to reproduce a simple monohybrid ratio, in which the heterozygous plants tend to follow the percentage relation, it seems at first that we are dealing with a case of multiple factors, in which one primary factor pair determines the hulled or hull-less condition and the other factors influence the hulled condition of those plants only that are hetero-zygous for the primary factors. This may be so, as the results of selecting high or low individuals seem to indi-cate. If, however, we assume a multiple factor series to

account for the facts, it is evident that, assuming all the factors involved to have equal value, we must have an F_1 type that is very nearly intermediate as regards its percentage condition. This we have not observed in any of our series. The F_1 type, while being generally intermediate, is not so as regards its hulled condition, for it always contains fewer hulled kernels than hull-less. Thus, so far as the percentage relation is concerned, we do not have a strict intermediate. To be sure, there is a reduction of the multiple-flowered spikelet and other changes which cause the F_1 type to appear as an intermediate.

With the usual multiple factor hypothesis assuming ordinary segregation, there must be a larger number of individuals ranging from 30 to 70 per cent. than we have at the extremes. With series 379 and 202 we do not have any indication of such a condition. On the other hand, there is a slight suggestion that series 382 does tend more nearly to a frequency distribution such as would usually be expected with the ordinary multiple factor hypothesis. When the third generation distribution of series 202 is observed (Correlation Table V) it is apparent that there is more of a tendency to pile up nearer the lower values. When the size of the classes is doubled a decided skew curve is obtained with the mode at class 0–9.9. As stated above, the seed sown to obtain the plants used in this distribution was selected from plants of high, low, or medium value, and this may influence to some extent the type of distribution. Yet, when one examines the percentages of the plants used as parents, it is apparent that they are fairly evenly distributed. If, as suggested above, the nearly dominant primary factor pair influences the hulled or hull-less condition and the other factors influence the hulled condition of plants heterozygous for the primary factor, then we would expect a piling up near the lower values.

With series 382 there is a tendency for both the third and fourth generation percentage distributions to be

grouped around the middle classes. This is especially true with regard to the fourth generation, especially when the size of the classes is doubled.

The results of the different series are rather conflicting and it does not seem possible at present to explain all of them on a simple multiple factor hypothesis. It seems quite possible to explain series 382 on this basis (except the first generation) but the other types do not at present seem capable of such an explanation.

The distribution in Table II, which is the third generation of a cross between Danish Island and Hull-less, is skewed much the same as for the third generation of series 202. No doubt for these series there is some disturbing factor which causes such distributions and more data will be needed before a suitable explanation can be found to fit all of these cases. It may be that, since in crosses between two hulled sorts we have found some hull-less spikelets, we have combinations such that there is a tendency to produce an excess of hull-less kernels. This would influence the type of distribution considerably.

At first one might assume that those individuals nearer the lower part of the distribution were like the F_1 types, however, from all the plants tested where the percentage of hulled kernels has been low the frequency distribution of the percentage of hulled kernels from the heterozygous plants has been low in general and has not ranged from very low to very high, as would be the case with seed from F_1 plants. These facts would help support the statement just made, which is to the effect that it is possible certain crosses tend to produce an excess of hull-less kernels.

Summary

From the results presented it is evident that hull-lessness exhibits a simple Mendelian ratio of 1 hulled, 2 intermediate, 1 hull-less.

The intermediates show all gradations of hull-lessness from those nearly hulled to those nearly hull-less.

The percentage of hulled kernels on the heterozygous plants seem, to indicate to some extent the percentage of hulled kernels on the heterozygous offspring.

No matter what percentage of hulled kernels is present on the heterozygous individual, it tends in general to produce a 1:2:1 ratio.

The hulled and hull-less kernels from intermediate plants reproduce similar 1:2:1 ratios.

ENVIRONMENTAL REACTIONS OF PHRYNOSOMA[1]

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I. INTRODUCTION

1. *General Distribution.*—The horned lizards, more familiarly known as the "horned toads," of the southwestern portion of the United States and the northern states of Mexico form a very distinct group of the family Iguanidæ. Unlike most other comparatively large reptilian genera, this particular genus (*Phrynosoma*) is limited to a very special environment, and it is only in a region of relative aridity that these animals find a favorable habitat. Within the limits set by the above condition the specific habitats of the various species and varieties of the genus vary greatly, ranging all the way from the extreme aridity and great heat of Death Valley in southern California (*Phrynosoma calidiarum* Cope) to the comparative moisture and cold of the northern Rockies (*Phrynosoma douglassii* Bell and varieties). The species especially discussed in this paper are all found in the Southwest, under varying environmental conditions.

Phrynosoma modestum, the specimens of which were taken near Albuquerque, New Mexico, close to the lower edge of the "mesa" or clinoplane region, at an altitude of about 1,700 meters, is distributed throughout New Mexico, and to a certain extent in the adjoining states, wherever conditions are similar to those in the above typical habitat. The rainfall here averages about 30 cm. annually, while the yearly evaporation from a free water surface is in the neighborhood of 200 cm. The soil is

[1] Contribution from the Zoological Laboratory of the University of Illinois.

rather loose and friable, consisting principally of "Ti-
jeras fine sandy loam" and containing, near the surface,
a relatively large proportion of fine angular gravel and
wind-blown sand. The color is a yellowish or yellowish
brown. The vegetation is sparse, consisting of scattered
grasses, *Chrysothamnus, Gutierrezia, Salsola, Yucca,* etc.
This species is not found in the adjoining valley of the
Rio Grande, nor in the mountains (Sandias) which border
the "mesa" on the east (2,200 meters and above), where
moister conditions prevail. In the mountains the rain-
fall is probably twice as great, on the average, as on the
"mesa," although accurate data are not available, and the
evaporation is much less, due to the lower temperatures
which prevail. In the valley the water table is very near
the surface of the soil (actual soil surface or above to
5 meters below the surface). Standing water is not found
on the clinoplane except after very heavy rains, which
sometimes fail for months.

Phrynosoma douglassii ornatissimum, specimens of
which were obtained with the above, has a much less re-
stricted habitat, both locally and regionally. It is dis-
tributed over a great deal of the eastern slope of the
Rocky Mountains, even as far north as Canada, and,
locally, extends into both of the regions described above
as bordering on the clinoplane. It is, indeed, more abun-
dant in either of these than in the clinoplane region be-
tween, indicating that the determining factor in the dis-
tribution in this case is similar in the lower valley and
on the mountain side. As mentioned above, the aridity
of these two regions is much less than that of the clino-
plane. The soil differences are also marked, in that the
moister soils are more dense and contain more humus,
derived from the more abundant vegetation. However,
the variation in both regions is very great, from heavy
clay to fine sand in the valley and from native rock to fine
sand in the mountain.

Phrynosoma cornutum does not occur in the same local
area as that occupied by the species previously mentioned,

although it also is of wide distribution. This species is
found throughout Texas and eastern and southern New
Mexico, and has been reported from Nebraska, Arkansas,
etc. In general, it appears to inhabit regions in which
the mean summer temperature is slightly higher than that
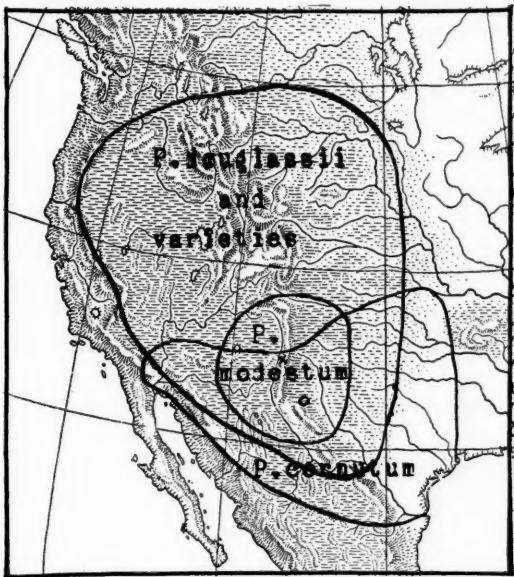
Map showing the approximate geographical distribution of the species discussed
in this paper.

required by the other two species. The specimens here
considered were obtained at Alamogordo, in the Otero
Basin, New Mexico, where the mean temperature is higher
by about 5° C. than at Albuquerque.

  2. *General Habits.*—The general habits of the three
species here considered are much the same, so no sepa-
rate description will be attempted. The following dis-
cussion will apply, perhaps, more accurately to *Phryno-
soma modestum* than to either of the other species, but
will, in general, be true of all. They are not, essentially,
heat-loving animals, although tolerant of desert condi-

tions. They are found more abundantly during the
earlier summer months, and during the autumnal rainy
season, when the aerial temperature does not exceed 32°
C. During these periods the animals move about actively
all day, spending the night in protected nooks under
vegetation, in the burrows of other animals, or buried
beneath the surface of the soil. As the daily maximum
temperature becomes greater they are to be found only
in the early morning and in the later afternoon when the
heat is less intense. During the heated part of the day
the lizard is at rest, almost if not quite buried under the
superficial layers of the soil. This position is reached in
a characteristic manner. The snout is directed down-
ward and moved rapidly from side to side, the body ex-
tremely flattened, while the legs take part in a rapid hori-
zontally clawing movement. The net result of this series
of movements is to cover the animal with the loose soil,
the depth varying according to the temperature, the char-
acter of the soil, and other external conditions, as well as
the individual. The same method of burrowing is em-
ployed in preparation for hibernation, when the animal
may bury itself under several inches of loose soil. In at-
tempting to escape from enemies, other lizards have been
observed to dig in a similar manner, and it is probable
that *Phrynosoma* also escapes in this way.

3. *Food Relations.*—The food consists of various in-
sects with which the animals come into contact, ants being
more readily eaten by the smaller individuals and beetles
(*Eleodiini*) forming a considerable portion of the diet
of the larger ones. No food is taken unless it is living or
at least moving. Sand grains set in motion by a heavy
wind or otherwise are often snapped up, and sand grains
are accordingly found in the feces.

4. *Water Relations.*—None of the species of *Phryno-
soma* have been observed by the writer to drink water,
and it is doubtful if water, independent of that contained
in the insect food, is ever ingested. Many individuals are
found in situations where there is never any standing

water except after the very infrequent heavy rains. Very little water is excreted ordinarily, as when fed on ants, beetles, etc., the feces are eliminated as a dry mass containing practically no water, and the urine is composed of an equally dry mass largely made up of crystals of uric acid. When fed on a moist diet, such as grasshopper nymphs from a moist habitat, the feces become softer and are often accompanied by a considerable amount of mucilaginous liquid. The urine, however, remains as usual. The idea that the excretion of waste nitrogen as uric acid is an adaptation on the part of the Reptilia for life in arid regions is well borne out by the conditions in these animals. Urinary analyses made by the writer in the laboratory of physiological chemistry of the University of Illinois give the following results (1917b):

Constituents	Milligrams per gram
Total nitrogen (N_2)	260.0
Ammonia nitrogen	1.4
Urea nitrogen	0.0
Uric acid	765.0
Uric acid nitrogen	255.0
Ash	87.5
Phosphorus as P_2O_5	3.5

It will be observed that uric acid accounts for practically all of the nitrogen contained in the urine and that urea is entirely absent. In this respect the urine of the horned lizard differs from that of the aquatic and semi-aquatic reptiles, which contains a considerable amount of urea, as does that of birds, another group in which the uric acid content is high.

5. *Reproduction.*—It is in connection with *Phrynosoma cornutum* that the long-disputed question as to the viviparity or oviparity of the members of this genus may be opened again. Cope (1898) states that *Phrynosoma* is oviparous, which is denied by Ditmars (1908) and Watson (1911), the latter of whom bases his statement on observations of *P. douglassii*. On July 5, 1917, some twenty specimens of *P. cornutum* were received at the vivarium

of the University of Illinois from Alamogordo, New
Mexico, and placed in a sand-bottomed wire screen cage.
On July 7, between 11 A.M. and 1 P.M., twenty-three eggs
were deposited in the sand on the bottom of the cage.
The eggs were about 1 cm. in length, ovoid in shape, and
covered with a grayish-white shell of leathery texture.
Some were opened and found to contain living embryos
of about 2 mm. length.   Several times thereafter, during
a period of two weeks, eggs were found in the cage, always
lots of about twenty.   The deposition of the eggs was
never observed.   None of the eggs hatched, although liv-
ing embryos were found in eggs opened a week after
deposition.   Such embryos were about 6 mm. in length.
P. douglassii has not been observed to lay eggs, although
a few eggs of *P. modestum* were discovered in the cage
in which these animals were kept.   These were found in
small numbers only and differed from those just de-
scribed in being light yellow in color and having no
leathery shell.   They were probably abortive.   As the
observations of Watson and Ditmars appear to be well
founded, it is possible that the genus is divided with re-
spect to the retention or deposition of the eggs, or that
in the same species different conditions may alter the
length of time the egg is retained in the maternal body,
as is the case among the adders.

II. Environmental Factors

As has been concluded (1917a), it is dangerous to as-
cribe to any one factor or group of factors the supreme
rôle in determining the seasonal or general distribution of
a species.   These factors are certainly not the same for
all species even in the same environment, and before defi-
nite conclusions can be drawn a careful analysis of the
habitat must be made, and experimental data must be ob-
tained as to the reactions of the animals in gradients in-
volving the factors capable of variation.   Unfortunately,
it is not possible or practicable to construct effective

gradients involving all environmental conditions, and in such cases we must rely on careful observation and analysis. Such a review as has just been given of the habitat and habits of the horned lizards may indicate to us the probable external conditions variations of which are of importance in the daily and seasonal life of the individual and of the species. The following are the most apparent of such external conditions:

1. Temperature.
  - (*a*) Air.
  - (*b*) Soil.
  - (*c*) Maxima and minima.
2. Water.
  - (*a*) Relative humidity and evaporating power of air.
  - (*b*) Soil moisture.
  - (*c*) Food in relation to its water content.
3. Soil.
  - (*a*) Texture as influenced by
    1. Composition.
    2. Moisture content.
    3. Vegetation.
  - (*b*) Color.
4. Food.
  - (*a*) Character.
  - (*b*) Abundance or scarcity.
5. Light.
  - (*a*) Quality.
  - (*b*) Quantity.
  - (*c*) Rhythm.

In the natural habitat it is rare that one of the above conditions varies without an accompanying variation in one or more of the others; for example, a variation in temperature of the air is accompanied by a variation in the relative humidity and in the evaporating power of the air, and may be followed by an alteration of soil temperature and soil moisture, as well as soil texture. Thus it is difficult to consider these conditions separately.

1. *Temperature.*—That temperature affects profoundly the daily life of the animal and limits its activities is shown by the relation of daily variation in temperature to the change from diurnal to crepuscular habit and to the burrowing activities initiated by high or low temperatures. Minimum temperature is probably associated most closely with the phenomena of hibernation. According to Bachmetjew (1901) the minimum winter temperature which can be survived by hibernating insects depends on the degree of elimination of water from the tissues and the consequent lowering of the freezing point of the body fluids. Tower (1917) states that in the case of potato beetles those animals acclimated to desert conditions (retention of water) are killed at higher temperatures than those of a more humid climate. In the experiments to be described gradients in air temperature and in soil temperature (substratum temperature) were established and the reactions of animals in such gradients were recorded.

2. *Water.*—The water relation must always be important in an animal adapted to arid conditions, even though this relation may seem to be negative. As indicated by the examination of excreta and observation of the water relations of *Phrynosoma* it would appear that the absence of water as such would not have a limiting effect on the distribution of the animals. It is probably necessary, however, that a certain minimum amount of water be supplied in the food, and that the evaporating power of the air must not exceed a certain maximum for any great length of time. It is to be doubted that any vertebrate may subsist indefinitely without some small water supply in addition to metabolic water. As shown in previous experiments (1917a), the reaction of *Phrynosoma* in a gradient of the evaporating power of air is not definite unless the gradient be very steep. Daily variation in the normal habitat is very large.

3. *Soil.*—The apparent importance of the burrowing reaction in the life history of the members of this genus

points to a corresponding importance of the texture of the soil. Evidently this must be such as to render the success of the burrowing reaction comparatively easy, a condition which is met only in soils of a low moisture content, and little humus, containing a considerable amount of loosely aggregated particles of sand or fine gravel. In a heavy clay or loam it would be impossible for the animal to burrow deep enough to get below the zone of killing temperatures during hibernation. This would also be impossible in a compact sod. Unfortunately, the problem of the soil relation involves an extensive seasonal study which, so far, it has been impossible to carry out.

While the color and markings of the animals vary with the individual and the species, and the color of the individual changes from time to time, it may be said in general that the color of the horned lizard is very similar to that of the soil of its normal habitat. Experiments of the author and others have shown that high temperature, darkness or high evaporating power of the air causes a centripetal movement of the melanophoric pigment, while the opposite conditions cause a darkening. Thus, in general, individuals observed after a rain are darker in color than at other times. The soil is also darker when wet, which might lead the observer to suppose that the change had taken place as a direct adjustment to the color change of the substratum, while the actual cause is the change in the evaporating power of the air. Within the limits of the conditions of the habitat, variations in the evaporating power of the air are the most potent factors in the production of color changes. No direct connection between the color of the animal and that of the substratum has been verified experimentally by the author. Redfield (1917), in a recently published paper on the color changes in *Phrynosoma cornutum*, has stated that there is a direct approximation of the color of the animal to that of the substratum, and that the light rays reaching the retina form the stimulus for such changes. The mechanism for

the approximation of the color of the animal to that of the
substratum is, according to Redfield, subordinate to the
daily rhythm of color change occasioned by changes in
light and temperature, and to changes brought about by
the emotional condition of the animal.

4. *Food.*—An adequate study of this factor would re-
quire much more extended observation than has been pos-
sible. Some suggestions as to the character of food re-
quired have been made above.

5. *Light.*—An estimation of the effect of light of vary-
ing intensity and quality in the natural habitat would be
very difficult, but it is probable that the relations of light
in the life of such animals have been greatly underesti-
mated. Experiments with a gradient of the color of light
are included here.

III. Experimental Results

1. *Air Temperature Gradients.*—Two series of experi-
ments were performed in which air varying in tempera-
ture was passed across the experimental cage previously
(1917a) described. In the first series the air passing
across one third of the cage was heated to a temperature
of about 38° by being passed through coils immersed in
hot water, that passing across the next third was heated
to about 33°, while the remaining third was supplied with
air at about 29°. The air was unmodified except as to
temperature and the rate of flow was the same in each
case. Typical results of this series (*Phrynosoma mo-
destum* only) are shown statistically in Table I.

In the second series the air for the hottest third was
heated to a temperature in the neighborhood of 50°,
which is about the maximum soil surface temperature on
unprotected sand exposed to the direct rays of the sun.
This temperature was obtained by passing the air through
heated iron pipes. A medium temperature was obtained
by passing the air through coils immersed in hot water,
as above, while the lowest temperature was that of the

TABLE I

EXPERIMENT 34. SHOWING THE REACTIONS OF *Phrynosoma modestum* IN AN AIR TEMPERATURE GRADIENT

Ten animals were placed in the cage, and observations of their position taken at one-minute intervals. The temperatures taken at intervals along the cage are indicated at the heads of the respective columns.

Minutes	Temperatures					
	Experiment 34a			Experiment 34b		
	29°	33°	38°	38°	33°	29°
1	3	3	4	3	4	3
2	4	2	4	3	5	2
3	4	2	4	3	6	1
4	4	2	4	4	4	2
5	3	2	5	4	4	2
6	3	2	5	4	5	1
7	3	4	3	4	5	1
8	3	4	3	4	5	1
9	3	4	3	4	5	1
10	3	4	3	4	5	1
11	3	4	3	4	5	1
12	4	3	3	4	5	1
13	2	4	4	4	5	1
14	2	4	4	4	4	2
15	2	4	4	3	5	2
16	2	4	4	3	5	2
17	2	4	4	3	5	2
18	2	3	5	4	5	1
19	2	3	5	4	5	1
20	2	3	5	4	5	1
21	2	3	5	5	4	1
22	1	5	4	5	4	1
23	1	5	4	5	4	1
24	1	5	4	4	5	1
25	1	5	4	3	6	1
26	1	4	5	3	6	1
27	1	4	5	3	6	1
28	1	4	5	3	6	1
29	1	4	5	3	6	1
30	1	4	5	3	6	1

unmodified air, about 30°. These temperatures varied somewhat in the various experiments, as shown by the records, but were fairly constant throughout a single experimental period.

The records of Experiments 34a and 34b show, for *Phrynosoma modestum*, that the optimum air temperature is in the neighborhood of 35° or 36°. The graphic records of Experiments 86 and 88 (Pl. I) show similar results. It will be noticed in the record of the former
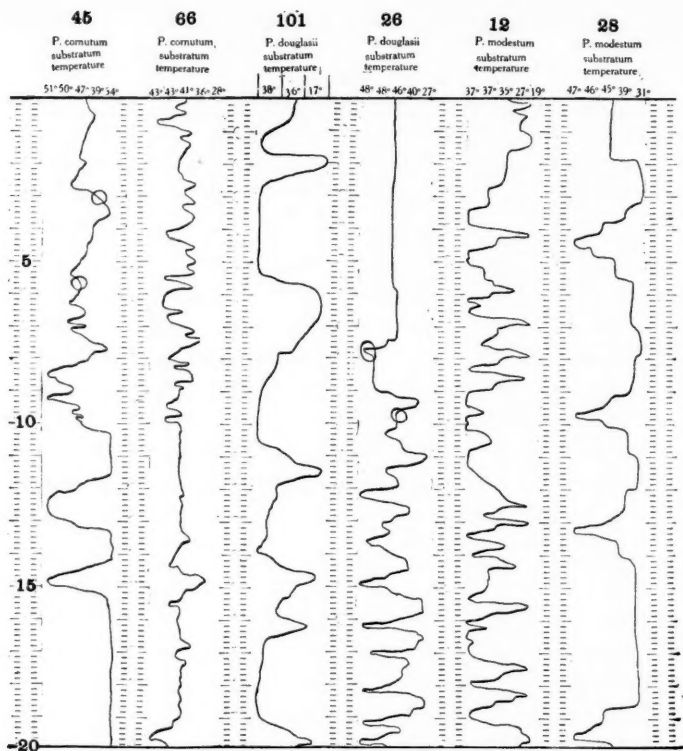
PLATE I. Illustrating the reactions of *Phrynosoma* in gradients of air temperature and substratum temperature. Experiments No. 45, 66, 101, 26, 12, 28, 86, 88, 82, 85, 78, 81.

In the chart, each section between the numbered scales represents the record of a twenty-minute experiment, the distance between the scales representing the length of the cage, and the vertical length of the chart the time, twenty minutes, each division on the scale representing ten seconds. The curve represents the movements of the animal under observation, and as the time component is vertical and the space component horizontal, the parts of the curve most nearly horizontal represent the most rapid movements, while the vertical parts of the curve indicate that the animal remained in the same position during the length of time indicated on the adjacent scale. The character of the experiment is in each case noted above the graph, as is the temperature of the various parts of the cage. In some the temperature was taken in five places along the cage and in others in only three places, as indicated. The circles found in the graphic records of certain experiments indicate that the animal attempted to burrow at the times indicated.

Controls, *i. e.,* experiments in which all portions of the cage were at the same temperature, were carried out in all cases, but the regular curves obtained have been omitted to save space.

Experiment 45.—For the first two minutes the animal was comparatively quiet, and after the close of this period moved toward the hot end of the cage, to return immediately, and then attempted to burrow. Just after the fifth minute the animal again moved toward the higher temperature and again burrowed. Thereafter the movements were of greater amplitude but less frequent, until the animal finally came to rest near the cooler end of the cage, where it remained until the end of the experimental period.

86	88	82	85	78	81
P. modestum substratum temperature	P. modestum air temperature	P. douglasii air temperature	P. douglasii air temperature	P. cornutum air temperature	P. cornutum air temperature
50° 38° 30°	49° 38° 31°	48° 38° 31°	45° 38° 31°	50° 40° 30°	52° 40° 30°
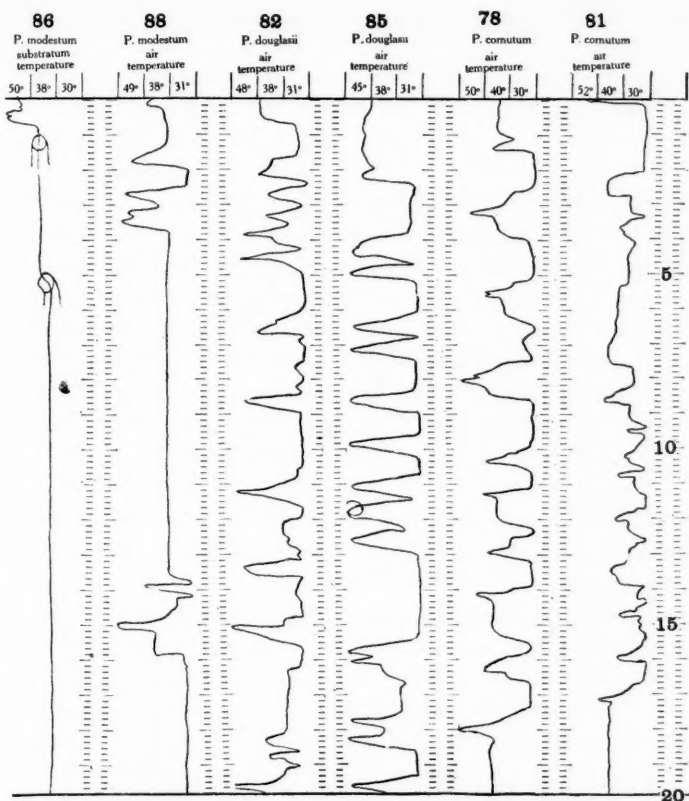
Experiment 66 shows a record of almost the same character, except that all movements were of lesser amplitude.

Experiment 101.—*Phrynosoma douglassii* here remained for the greater part of the time at a temperature of about 38°, making infrequent excursions into the region of lower temperature.

Experiment 26.—Same species as above. The temperatures here were higher, and the animal avoided the highest temperatures.

Experiments 12 and 28 show results similar to the two just preceding, in one the avoidance of low temperatures and in the other the avoidance of higher temperatures.

Experiment 86.—This is the record of the movements of a very sluggish individual, which burrowed twice at a temperature a little above that chosen by other members of the species.

Experiment 88.—This animal showed alternate periods of rest at an optimum temperature and activity involving incursions into both temperature extremes represented in the gradient.

Experiments 82 and 85 are good examples of the type in which there is great activity, but very short stays in the unfavorable temperatures.

Experiment 78.—This record shows avoidance and turning away from the higher temperatures. The farther the animal penetrated into the high temperature area before turning, the longer was the subsequent inactive period in the region of optimum temperature.

Experiment 81.—This animal was very sensitive to the higher temperatures and never reached the hot end, although very active at times.

that the animal burrowed, first at a temperature of about 38° and later at a slightly lower temperature (indicated by the circles in the first and sixth minutes of the record). This burrowing reaction was found to take place very often, throughout the whole series, usually at the upper limit of the optimum temperature range. This agrees with the phenomena observed in the field, of burrowing as the air temperature rises in the course of the day.

Phrynosoma douglassii, as shown in the graphic records of Experiments 82 and 85 (Pl. I), seems to choose a somewhat lower temperature, between 30° and 35°, although there is a considerable amount of individual variation.

Phrynosoma cornutum, the behavior of which in the gradient is illustrated by the records of Experiments 78 and 81 (Pl. I), appears to show a preference for a temperature slightly higher than that shown by the other species.

2. *Substratum Temperature Gradients.*—For the purpose of establishing this gradient the cage was placed in a water bath so arranged that hot water flowed into the latter at one end and cold water at the other, the water being directed backward and forward beneath the cage, and running out near the center, in such a manner as to produce a gradient in the temperature of the cage bottom. The temperature of the substratum was taken at intervals along the edge of the cage by thermometers whose bulbs were just covered by the sand in the bottom.

The statistical records of Experiments 43, 126 and 127 (Table II) show an optimum substratum temperature for *Phrynosoma modestum* of about 40°, or about 5° higher than the optimum air temperature for the same species. In this species the response to changes of temperature of the substratum is very definite, and by varying the temperatures of the gradient, the animals can be driven repeatedly from one end of the cage to the other as the temperature is raised or lowered. The lizards often burrowed at or near the upper limit of the optimum temperature, and, less often, at the temperatures below the

optimum.   The graphic records of Experiments 10 and 28 (Pl. I) show similar results.

TABLE II

EXPERIMENTS 43 AND 127. SHOWING THE REACTIONS OF *Phrynosoma modestum* IN A GRADIENT OF THE TEMPERATURE OF THE SUBSTRATUM
The method of recording is the same as that employed in Table I.

| Minutes | Temperatures | | | | | |
| | Experiment 43 | | | Experiment 127 | | |
	45°	41°	36°	25°	40°	52°
1	2	4	2	2	6	2
2	2	4	2	1 *1**	8	0
3	2	4	2	1 *1*	8	0
4	2	5	1	*1*	8	1
5	2	5	1	*1*	8	1
6	2	4	2	*1*	8	1
7	2	5	1	*1*	8	1
8	3	4	1	*1*	9	0
9	1	6	1	*1*	9	0
10	1	5	2	*1*	9	0
11	1	5	2	*1*	*1** 8	0
12	2	5	1	*1*	*1* 8	0
13	2	5	1			
14	1	6	1			
15	1	5	2			
16	1	5	2			
17	0	6	2			
18	0	6	2			
19	0	6	2			
20	0	7	1			

* The individuals indicated by the *italic numerals* burrowed in the space indicated.

The individuals of *Phrynosoma douglassii* gave practically the same figures for the optimum substratum temperature.   The graphic records of Experiments 101 and 26 indicate the behavior of this animal in the gradient. Statistical records of the behavior of *Phrynosoma douglassii* and *Phrynosoma cornutum* in this gradient were not made, because of the size of the animals, which prevented the introduction of any number into the cage at the same time.

Phrynosoma cornutum, as illustrated by the records of Experiments 45 and 66 (Pl. I), chose a higher substratum temperature than either of the other species, averaging nearly five degrees above that shown by the other curves.

In summing up the results of the air temperature and substratum temperature experiments (over one hundred) in relation to those of the evaporation gradient previously reported (1917*a*), it is found that the animals choose conditions which are very near the normal conditions in the usual habitat at the time of the greatest activity. These conditions represent the optimum for the animals. For example, as reported in a previous paper, the evaporation optimum for *Phrynosoma modestum* appears to be near 3 c.c. per hour, as measured by the standard atmometer, which is very near the average outdoor evaporation as observed in the natural habitat of the animal at the season and at the time of day when the animal is most active. If the temperature under such conditions be observed, it will be found that the average atmospheric temperature, 1 cm. from the surface of the soil, in the sun, is in the neighborhood of 35°, and that of the surface layer of the soil about 40°. These temperatures vary greatly, of course, with other features of the weather, such as air movements, clouds, etc., but the above figures represent a normal condition. Of the variables mentioned here, substratum temperature has much the greatest effect on the behavior of the animal.

3. *Moisture of Substratum Gradient.*—Although it was impossible to establish and observe an effective gradient in general soil conditions, several experiments were performed on the direct effect of a soil moisture gradient. The gradient in water content of the substratum was obtained by placing a layer of torpedo sand saturated with water on the bottom of one third of the cage, a mixture of saturated sand and dry sand in the adjoining third, and dry sand in the remainder of the cage. In none of the species observed was any marked preference for any portion of the cage exhibited. Soil moisture, as such, does not seem to affect the movements of the animals, although, in the natural habitat, the high evaporating power of the air produces a considerable degree of temperature difference between dry soil and wet soil by the

vaporization of the water from the latter. This difference was not reproduced under experimental conditions. Typical results of this series of experiments are shown in the graphs of Experiments 91 and 97 (Pl. II).
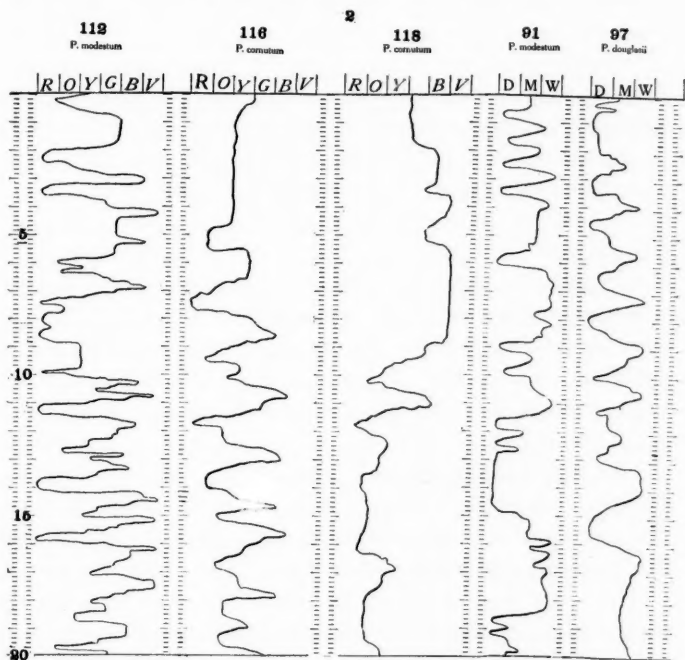
PLATE II. Illustrating the reactions of *Phrynosoma* in gradients of wavelength (color) of light and moisture of substratum. Experiments 112, 116, 118, 91 and 97.

Experiment 112.—In this and the two experiments following, the letters *R, O, Y, G, B* and *V* above the graphs represent the color of the light screen over the corresponding portion of the cage. The graphs may be interpreted in the same manner as those illustrated in Plate I. In this experiment the animal avoided the violet section, turning away from it rather quickly in each instance, The greater part of the time was spent in the green and the yellow.

Experiment 116.—This animal avoided the violet and even the blue very markedly and entered the red only twice. The optimum seems to be in the yellow and the green.

Experiment 118.—Avoidance of both the violet and the red is characteristic of this curve. This animal, however, did not avoid the blue and the orange, in which it spent a considerable amount of time.

Experiments 91 and 97.—Here the letters *D, M,* and *W* refer to dry, medium and wet thirds of the cage. The graphs show no preference for either on the part of the animal.

4. *Gradient in the Color of Light* (*Wave-Length*).— Although it would be difficult to estimate the effect of the various light components in the natural habitat, a series of light experiments has been included. For use as a color gradient the cage used in the other experiments was covered with an accessory lid composed of a series of six equal strips of gelatine ray filter in the principal colors (violet, blue, green, yellow, orange, red). Three forty-watt electric lamps were placed above the cage within the observation hood, so that the light was approximately equally distributed throughout the cage, each sixth being illuminated principally by rays of a narrow range of wave-length.

Experiment 112 illustrates the movements of *Phrynosoma modestum* in such a gradient. The longest rays were avoided, as well as the shortest, although the animal remained for greater lengths of time in the red section than in the violet. The optimum seems to lie in the green and the yellow.

Phrynosoma cornutum (Experiments 116 and 118, Pl. II) avoided both red and violet, with an optimum near the middle of the spectrum. *Phrynosoma douglassii* did not respond regularly and seemed little affected.

The color reactions are probably not as significant as those involving some of the other factors here considered. Direct sunlight in the arid regions contains a rather larger amount of the light of the shorter wave-lengths than elsewhere, and it is possible that the avoidance of violet light as shown in these experiments is of significance in explaining the avoidance of sunlight under certain conditions, but it is more probable that temperature is the dominating factor in this reaction.

IV. Summary and Conclusions

1. Of the temperature conditions capable of being tested in the gradient, the temperature of the substratum calls forth the most definite response. In addition to the

indication of an optimum by the movements of the animal, definite motor responses of a specialized character (burrowing) are made to certain temperature conditions just above or just below this optimum. The temperature of the air calls forth similar reactions but not as readily or as definitely as that of the soil, the reaction to the former being overshadowed by the response to the latter when a difference exists. The temperature of the substratum is evidently of very great importance in the daily movements of the horned lizards, and probably plays an important rôle in the control of distribution. The temperature of the soil is probably also of great importance in connection with the deposition and hatching of the eggs in those species which are oviparous. The differences between the optimum temperatures of the various species considered are in the direction and of the magnitude of the temperature differences normal to their respective habitats. While the limits of temperature variation favorable for the completion of the life cycle of the animal could not be subjected to experiment of the type here used, it is evident that at least the minimum is of great importance in connection with the phenomena of hibernation, and the maximum is probably of similar importance in relation to the estivation which takes place more or less regularly.

2. In the gradient of the evaporating power of air definite responses were obtained only in the case of one species (*Phrynosoma modestum*), and here only when the gradient was steep. The daily and seasonal variation in this factor is very large in the natural habitat. The reactions of the animals to temperature changes act in such a way as to prevent the exposure of the organism to excessive desiccation. The effect of soil moisture is felt indirectly, through the alteration of the temperature and the texture of the soil, the latter of which is important in relation to the burrowing habit. It is probable that there is a certain minimum water content of food, below which the animal can not survive. This must be very

low, however, considering the character of the normal food. The excretion of water is reduced to a minimum by the character of the nitrogenous excreta, which are almost exclusively in the form of insoluble uric acid.

3. An important factor in the distribution of these animals is the texture of the soil, which must be suitable for burrowing, as this is the reaction of the animal to unfavorable conditions generally, and specifically to temperatures inducing hibernation and estivation. The soil texture is affected adversely by increases in moisture content, and by increases in the amount of vegetation present. The color of the soil is probably important from the standpoint of invisibility and it is probable that there is some degree of approximation of the color of the animal to that of the substratum. It is difficult to see how this fact could be of much use to the animals, especially in the case of such profusely armored species as *Phrynosoma cornutum*.

4. The rôle of light in the daily and seasonal life of the horned lizards has not been shown, although they are positively phototactic and avoid extremes in a color gradient. The optimum in this gradient lies in the green and in the yellow. This may be correlated with the predominant colors of soil and vegetation in the natural habitat.

V. Acknowledgments and Bibliography

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MIGRATION AS A FACTOR IN EVOLUTION: ITS ECOLOGICAL DYNAMICS, II.

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III. THE MIGRATIONAL FACTORS IN EVOLUTION

1. Introductior

From the preceding discussion of the principles of animal activity which underlie their behavior, attention is now directed in greater detail to suggestions for their application to migration. Emphasis is placed upon those relations which show the main causes of stress, the cycles of circulation caused by diversity, and the interaction, equilibrium, and adjustment operating between the various systems. I have not attempted to go into detail on the quantitative relations, although there is much physical and some ecological data, already organized, which illustrate the method of application. There is, however, but little quantitative distributional data which are at present available. The elaboration of this phase is urgently needed. Limiting factors retard and prevent the migration and diffusion of animals; these are the "barriers" so frequently mentioned by students of geographical distribution. As previously mentioned, two major systems or agencies are involved in this process, the animal and the environment. The locomotor activity of the animal is a phase of its general responses. The migrations of most animals are therefore not different, in any important features, from the ordinary daily life of the animals; that is, migrations are incidental and included within the ordinary responses. Anticipating somewhat, and speaking broadly, if animal responses are of evolutionary value

so must be the migratory ones. In detail there are innumerable animal peculiarities which influence migration, depending on the stage of development of the animal, its physiological and ecological conditions and characteristics, and the status of its environment. The large number of factors involved in this is no doubt an important conservative influence and checks the speed of interaction.

The word migration is used in several senses, so that for our purpose it is now necessary to define this more definitely. By migration is here meant the movement of animals from one place to another, and this includes, not only the causes and conditions of their migration, but their methods as well and the immediate result upon the animal. If all migrating animals perished at the end of their journey the study of its influence would be relatively simple.

In deference to those who are mainly interested in the animal and who are less interested in the environment it has been customary in many zoological writings to discuss animals first, and their environment later. But as zoology progresses and as explanations are resolved more and more into the sciences upon which it rests, greater and greater prominence is given to the physical causes and conditions of the environment. Viewed broadly, zoology should be made to fit into the general world system in such a manner as will best aid in understanding it, irrespective of our traditional habits of mind. For this reason this phase of the discussion will begin with the environment, as a factor in *passive migration or transportation,* and will lead up to the animal as a factor in its own migrations.

In the orientation of the major features of the world Powell recognized: the atmosphere, the hydrosphere, the lithosphere and the biosphere. These self-explanatory, relatively homogeneous, physically and mechanically distinct, and interacting systems, furnish the medium in which animals live and perform their migrations. We

may look upon these three physical systems as a result
of existing temperature conditions of the earth. Increase
the temperature to a certain amount and the atmosphere
would be rarefied, the hydrosphere would disappear into
the atmosphere as water vapor, and the solid earth would
become fluid. Or, reverse the process, beginning with its
present state, and should the earth cool progressively,
the hydrosphere would become frozen to the solid phase
and atmosphere would likewise be transformed to
the solid state, and all these systems would become one.
The present resolved and differentiated state is thus de-
pendent on the present temperature conditions. The re-
lation of equilibria between these three systems is one of
the major problems for the application of the phase rule,
and their methods of interaction is an unlimited field for
the application of Bancroft's law, and both of these are
of the greatest importance to all concerned with the gross
environments of organisms.

In view of the dominating influence of temperature, we
must not overlook the fact that temperature is only one
of the essential conditions of life. It is important to ob-
serve that the present stratum of the earth's surface
where organisms live is a remarkably narrow one, and
only moderate departure above or below the condition in
this stratum at once becomes limiting factors to organic
activity. Chamberlin ('06, pp. 1–2) states this impres-
sively as follows:

The narrowness of the range to which temperatures must be confined
to permit progressive organic and intellectual evolution takes on its true
meaning only when we recall that the natural temperature range on the
earth's surface is sixteen times as great as this, while that affecting
the solar family is at least sixty times as great. For a hundred million
years, more or less, this narrow range of temperature has been main-
tained quite without break of continuity, unless geologists and biologists
are altogether in error in their inductions.

The maintenance of such a dynamic system of equilib-
rium of the environment and of the organism, and the in-
ertia of their systems—the tendency to continue or per-

sist in a given state—may well cause wonder and stimulate thought.

In the following analysis of the larger units which influence migration, those agencies will be used which serve as the basis for the smaller systems of action, and some of their main cycles of activity and methods of interaction will be indicated briefly.

2. Atmospheric Agencies in Transportation

The instability of the air, its numerous cycles of activity or circulation, hourly, daily, seasonally, annually, and those of longer duration, furnish an agency which has transported animals from one locality to another for ages. Gentle breezes carry small animals, while violent tornadoes carry larger ones. Small eggs, desiccated rotifers, entomostraca, and other small aquatic animals, have been transported long distances by the wind, and have thus found many favorable habitats, otherwise not available to them. The wind, reinforced by streams, even temporary ones, has transported animals long distances, as have the waves of the sea and inland waters. The winds, supplementing the flight of animals, have carried them thousands of miles beyond their normal range, as in the case of birds and insects. A vast literature has grown up recording the details of these findings, and yet about the only evolutionary conclusion which can be safely drawn from the multitude of facts is that by these processes animals have tried out and acclimated themselves to a vast number of isolated habitats which have tended to give them a varied and widespread range, and to that degree it has aided in their perpetuation.

The most definite evidence of atmospheric influence in evolution is perhaps the direct influence of climate and of climatic changes. Fortunately, for our present purpose, and mainly through the researches of Chamberlin (1897–1901) and Huntington ('15, pp. vi–vii), secular climatic cycles have been investigated. Chamberlin has related these intimately to the changes in the hydrosphere

and lithosphere, and he has indicated their modes of interaction in a strictly dynamic manner. He shows that during a period of land elevation and mountain formation, with cold, dry, diverse climatic differences and zonal arrangements on land and with a deepening of the sea, these conditions tend to change progressively toward a moist, warm, uniform and tropical condition, which is related to the land equilibrium developed during baselevel on land, and a marine condition of extensive shallow seas. The process of adjustment to these strains beautifully illustrates Bancroft's law. It is not an accident that mountains are centers of origin and dispersal of animals, nor are they solely refuges where endemic forms escape the competition of the lowlands. Mountain regions in their elevation subject whole populations to severe climatic and other stresses of many kinds, depending on the physical and vegetational diversity of the region, and doubtless thus many animals become extinct, while others as individuals or as a race become acclimated to the new and changed conditions and thus survive.

It seems strange that, although dynamic principles are shown in almost ideal form in the unstable air, yet, as a whole, this phase of science seems to be somewhat backward in the formulation of the ideas of processes, so that their greater successful application is seen in geology. It appears that the reciprocal dynamic relations which exist between barometric lows and highs (both temporary and permanent) makes them dynamic centers of action (Fassig, '99) in a cycle of circulation and adjustment to stress. This idea is one which may profitably be extended to the interpretation of successive phases in the establishment of climatic dominance. The change from the Ice Age to that of the present, and the accompanying change of storm tracks (Adams, '09, pp. 45–46) are comparable to the seasonal change from winter to summer dominance, while passing through the transitional March weather stage. Furthermore, the summer and winter dominance are dynamic equilibria established by a balancing among

the various highs and lows (Adams, '15a, pp. 69–71).
These transitional periods illustrate Bancroft's law in
the process of establishing new relative equilibria. The
dynamic centers are to be looked upon as concentrating,
transforming and radiating centers, whose recognition
and cycles of activity are an essential part in the applica-
tion of Bancroft's law to the development of atmospheric
equilibria.

3. Hydrospheric Agencies in Transportation

The waters of the earth are more dense than the air
but are yet quite mobile, and undergo relatively rapid
cycles of circulation, both in the sea and in inland waters.

(*a*) *Marine.*—The great currents of the sea, the tides,
and the wind-formed waves, are very active agents in the
transportation of animals. Not only are marine animals
extensively transported, but also, in the long run, large
numbers of land kinds, as the animals on oceanic islands
testify, as shown by Wallace. And just as the processes
of erosion operate upon land, and tend to reduce such
areas to sea level, so the sea itself possesses its own
cycles of transformation of its bottom and shores, tend-
ing to flatten them out to the equilibrium of the deep sea
floor, transporting materials and redistributing them in
response to its stresses, eroding here, depositing there,
and always making changes in the conditions which not
only transport animals, but as well, by the migration of
the physical conditions, lead animals from one locality
to another. Land animals are largely influenced by the
surface conditions, while the marine ones are largely by
sub-surface conditions.

(*b*) *Inland Water Bodies.*—Bodies of inland standing
water, in their broad features, are smaller editions of the
seas, as far as their waves, circulation and transport-
ing powers are concerned. Their chemical character,
whether fresh or saline, has more influence upon animals
than the mechanics or their methods of circulation. The
most marked influence of the inland waters is their rela-

tively small area, isolation, even though they may overflow into streams. Inland waters are in general relatively ephemeral in character compared with marine waters, because with progressive erosion of the land they tend to become extinct through deposition and ultimate drainage.

(c) *Running Waters.*—The transporting power of running water is easily evident. The constant direction of flow, its duration (as some drainage lines are of extreme antiquity), and repeated transportation, have subjected animals again and again to new conditions, and carried them to new localities. Streams transport both land and aquatic animals and by their persistence, activity, and the thoroughgoing fashion in which they work over the land surface, are one of the most powerful agencies of transportation. Streams undergo changes depending on the dynamic status of the stream. The greater stress to which the stream is subjected by uplift, the greater its velocity and its relative transporting power, and the nearer it erodes to base-level, the less current and relative transporting power it possesses. Most animals counteract the transporting power of the stream by definite responses to the current, and thus maintain their position and are not carried away.

4. Lithospheric Agencies in Transportation

The lithosphere includes the solid earth, which to the ordinary mind is the ideal of stability. The transporting power of the solid is, however, usually at a very slow rate, but this is not always the case, because of the suddenness of fracture. The solid ice of the glacier moves slowly and yet travels long distances, but usually does not transport an abundance of animals. Avalanches move with greater speed, but they operate in rather limited areas. Landslides transport, slowly or rapidly, large masses of land containing animals. All of these processes are dominated by gravity, and tend to transport animals from a higher to a lower altitude. Perhaps

the most powerful motion of the solid earth is seen in the crustal movements, associated with the cycle of isostacy, which elevates and depresses the surface of the land in relation to sea level. In this is seen an essential condition which has made all land life possible, because without such movements all the land would have been washed into the larger dominating sea. The great land elevations, such as those which produce plateaus and mountains, have transported whole faunas, covering thousands of square miles, upward, and have subjected them to great stress, through long periods of time. Such elevations as arise in a region unfavorable to animals, may improve them, as in the case of high mountains, rising on a dry desert, but often such elevations, which are departures from the favorable thin surface stratum, are in the direction of unfavorable conditions and of limiting factors. Broadly speaking, depressions below sea level are similarly limiting to marine organisms, and these have operated on a magnificent scale. The mountain tops, like the deeps of the sea, are relatively animal deserts, both are extreme departures from the conditions which are normal to most animals.

The most rapid physical agency in the transportation of animals on land is the influence of running water and that of the wind. These forces operate in short cycles and intensively, in contrast with the movements of the solid earth.

Volcanic activity has probably been only a minor factor in the transportation of animals, although in a secondary way, in conjunction with other agencies, as currents of water, porous materials buoyed by air, may act as a raft in their transportation. But indirectly by building mountains, islands, etc., it has had an influence similar to that of the crustal movements of the earth in forming new habitats, and has thus had a powerful effect.

5. *Biospheric Agencies in Transportation and Migration*

(*a*) *Plants.*—The relatively sedentary and rooted condition of plants caused Cope to aptly call them "earth parasites." With this stable habit and the unstable environment, rooted plants have been forced to develop a line of fracture, as it were, between themselves and the environment, which has permitted them, by their exceptional powers of dispersal, to spread rather freely at some stage, and to thus scatter over much of the available surface of the earth. As far as the actual movements of plants are concerned, unaided by winds, waters, and animals, but solely by growth and similar movements, plants have probably had but relatively small influence upon animal transportation, although secondarily, by the spreading of vegetation and the changed conditions which this causes, they have permitted extensive transportation and migration of animals. The specific gravity of wood, its buoyancy in water, and the various sails, vanes, and structures which favor wind dispersal, and all the hooks and claws which help make various kinds of burrs, and the edible fruits which animals devour, all combine to favor transportation by wind, water, animals, and other active agencies. By these means, animals living within, or on such transported parts, may be buoyed and transported by waves, currents of water or air, and be carried by animals for long distances, and into new localities and conditions.

(*b*) *Animal Migration.*—The movements of animals which take them from one locality to another are exceedingly diverse. They vary not only with the character of the animal, at different stages in its life history both structurally and functionally, and also under varied environmental conditions. The fixed and sessile animals more nearly approach the conditions found commonly among plants, but among animals this habit is confined mainly to aquatic animals, that is, to animals living in a mobile medium, which transports them at some stage.

The most important character which influences the migration of animals is its own powers of movement. These movements are dependent upon the ecology and the physiology of the animal, its structure and its mode of response. The general principles of response have been discussed in the first part of this paper, where the systems of activity, the cycles of activity, the limits of activity, and the interaction of all systems was emphasized. All of these factors should now be recalled. Animals creep, walk, swim, and fly, according to the media in which they live, their structure, and their ecology, and the interaction of all these factors put limitations upon animal movements.

From the standpoint of function, animal movements and migrations have two main influences. By movement the animal subjects itself to new conditions, these conditions have a direct influence upon the animal, and change the direction or its internal changes, and it becomes acclimated or dies; or by its repeated responses and retreating movements, it escapes from the adverse conditions and finally comes to rest in a new relatively favorable condition (Adams, '15, p. 12). This monotonous cycle is repeated with all the variations which diversity of animals and diversity of conditions can produce, and in its essential features it is the same from Protozoa to man.

The geological age in which we live is one in which the land surface, relative to the sea, has accumulated uplift from former ages, and has been newly elevated, and as a result there are many high mountains, and the seas are relatively deep. These are conditions of stress, and the processes of adjustment to strain are in full operation. This is a period of relative diversity of the lands and of the seas, which favors diversity, both in the atmosphere and in the hydrosphere. With the elevation of the land, this diversity is shown both vertically and horizontally. Large areas lie at considerable altitudes and in their departure from the narrow mean surface

stratum, are subjecting many animals to stress, and to the process of acclimatization to the high altitude conditions. The climatic diversity shown vertically, also expresses itself longitudinally, by interference with free circulation of temperature, moisture, and other climatic factors, and tends to produce the varied climatic zones, such as tropical, temperate, and polar, as well as the diversity due to humidity. These diversities mean that many minor circulating systems are caused and consequently there are varied local wind systems, further favoring diversity. All of these influences tend to favor local or relatively limited migration, rather than the widespread dispersal of animals subjected to such conditions.

The hydrosphere is influenced similarly. The diversity of the lands favors diversity in inland waters, and the arid climates favor saline waters. Inland waters under these conditions tend to be isolated and varied. In the sea the deepened waters produce stresses similar to those on land produced by altitude, and the elevations and relative increase in the land area interferes with the circulation of marine waters and favors local differences and local stresses. With the deepening of the seas, the shallow waters are restricted and the littoral animals are under increased stress. It is seen, therefore, that the conditions dominant on a world scale are those of stress or strain, now in the process of adjustment. It should be observed that all spheres, the atmosphere, hydrosphere, lithosphere, and the biosphere are involved in the same general interacting process. It is only by viewing the subject broadly that we thus gain this perspective of the status of our own times.

We may now turn to certain details which will help to illustrate the application of these ideas to animal migration. The same grouping of influences will be used which has been applied in the preceding discussion of passive migration.

(a) *Atmospheric Influences.*—The atmospheric factors

which influence active animal migrations are mainly those which are dependent upon: chemical composition (largely oxygen, CO_2 and volcanic gases); temperature; pressure; humidity; and mechanical effects, as they are combined in climatic changes. All of these influences undergo differences which influence, by acceleration or interference, the movements and migrations, acclimatization and ecological attunement of animals. Furthermore, these influences, or their systems, do not act independently but at the same time, so that their laws of interaction are the main rules of the game.

(b) *Hydrospheric Influence.*—The hydrospheric influences are similar to those of the air, depending on: composition (salts and gases); temperature; pressure; and mechanical effects (waves, tides, circulating currents). In this geological age of stress and diversity, on account of the mobility of this medium, it has transmitted its pressure with slight friction to animals. Upon land the active streams are a direct response to the steep slopes down which they flow, and they visualize at once the reality of this active media which has kept fishes and other animals busy moving up stream for millions of years. Bodies of standing water, by their isolation, except when connected with streams, tend to retard active animal migration. Such bodies are likely to abound in the early stages of uplift and to decline as drainage lines develop. The diversity of climate into humid and arid as previously mentioned, tends to favor diversity, chemically, in bodies of standing water. These inland waters, while discontinuous to many aquatic animals, are not so to many flying and running kinds.

In the sea, the narrowing of the continental shelf tends to crowd the shore animals, and favors isolation and diversity of habitat, and retards ready migration for many animals. The hastened erosion, however, tends to increase the continental shelf and its continuity. The deeper water shows relative diversity and tends toward stagnation in its currents because of the relative increase of the land area.

(*c*) *Lithospheric Influences.*—The interdependence of the physical spheres is so marked that by this time, in the discussion of the air and water, the solid earth has been included in part. The rigidity of the lithosphere is so great that its adjustments to strain are in general relatively slow and of long duration. The density of the medium is so great that animals inhabit only a shallow surface stratum, the upper part of the zone of weathering processes, in or on the soil. Animals living in the soil are influenced by its density, its physical and chemical composition, temperature, and its movements. Those living on it are relatively independent of the qualities just mentioned, but are much influenced by the relief of the surface, by the climate and vegetation, and are more truly air rather than earth dwellers. The elevation of the land above sea in itself, and not as modified by climate and topography, probably has little direct influence, except in its degree of stability with regard to erosion. The greater the altitude and the steeper the slope, the greater the physical stress and the rapidity of erosion. Ice and landslides exert pressure and drive animals before them, and are largely dependent on elevation and slope. The cycle of degradation of the land, particularly its topographic diversity, greatly influences the degree of freedom in the movement of land animals.

(*d*) *Plant Influences.*—The stresses of the physical environment in the air, water and earth, impose pressure upon the vegetation. Since the largest number of animals are directly dependent, and a smaller number indirectly upon plants, much of this pressure is transmitted to animals. The climatic diversity, seasonal and secular cycles, influence the amount of animal food. Some animals, during adverse seasonal conditions and scanty food supply pass into an inactive state, and tide over such a season, and most animals not possessing such tend to migrate. Thus upon the plains the bison wandered with the seasonal changes of pasture, just as mountain sheep and goats migrate up and down the slopes as their pasture

varies with the season. The succession of vegetation upon all surfaces, drives out some animals, just as it invites others to follow with it, as when, with the development of forest, the animals of the open find conditions unfavorable. The kind of vegetation, whether herbaceous, woody, conifer or deciduous, etc., has an important influence upon the movements of many animals. The cycles of vegetation also change the physical conditions, the temperature, humidity, soil conditions, and thus influence animals.

(e) *Animal Migrations.*—The individual migrations of animals, caused by their own spontaneity, and that by
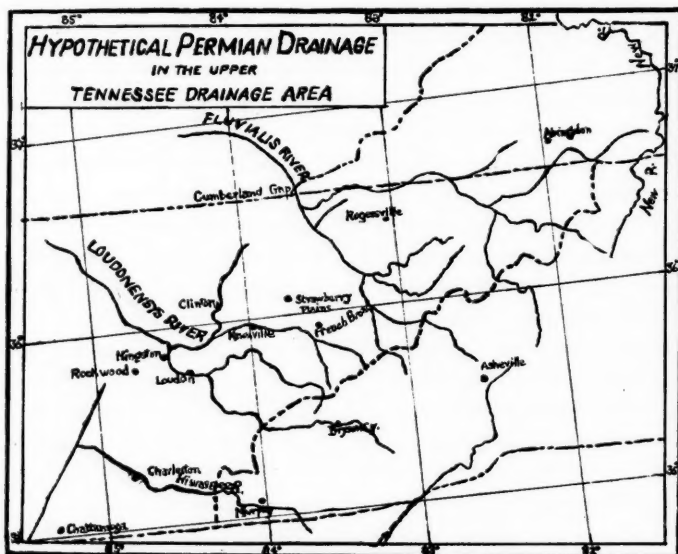
Fig. 1. Map showing the hypothetical Permian drainage of the Upper Tennessee drainage area. Compare with the present drainage shown in Fig. 2.

other animals, are exceedingly varied. All the factors which influence individual movements, as indicated in the first part of this paper, now apply in detail, and in addition there is the pressure exerted by animals living associated with them. Simple animals require a favorable

environment as truly as complex ones. It is known that
many animals decline in vigor if kept in the same medium,
but if the medium is kept fresh, or the animal moves
about freely and secures a fresh medium, it thrives.
Freedom of movement thus permits the animal to move
away from influences which interfere with its system, and
thus minimizes the disturbance. The continuation of
this process tends, with freedom, to bring the animal ul-
timately into favorable non-interfering conditions if
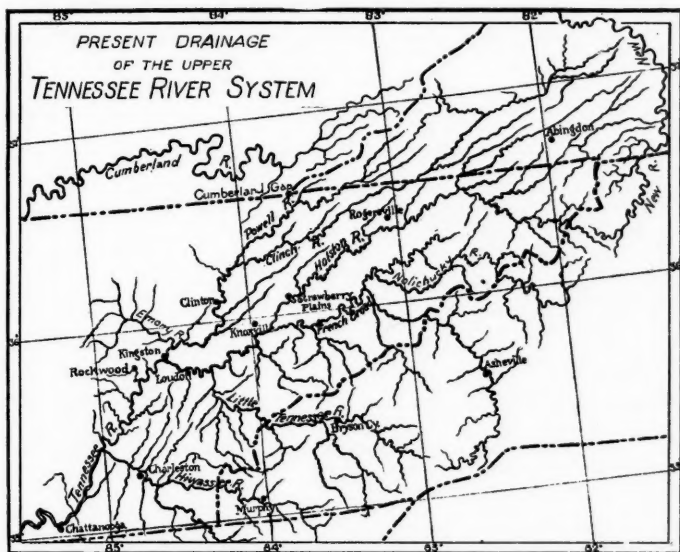
FIG. 2.   The drainage of the upper Tennessee River system.

such exist. With these ideas in mind we need to recall
that the atmospheric, hydrospheric, lithospheric and
vegetational pressure all combine to encroach upon the
animal, and to interefere or reinforce its activities and
movements. The normal movements of the animal, and
the ordinary routine of environmental changes, are thus
in process of continual adjustment. Thus with the mi-
gration of the animal habitat, whether caused by a change
in the atmosphere, hydrosphere, lithosphere, vegetation,

or any combination of these, the animals also tend to migrate with it and they are thus led about all over the surface of the earth. In this we see the importance of cycles of climatic changes, cycles of crustal movements of the earth, changes in circulation of the sea, and the succession of plant and animal associations. It is to the changes of this character that the student of paleontolog-
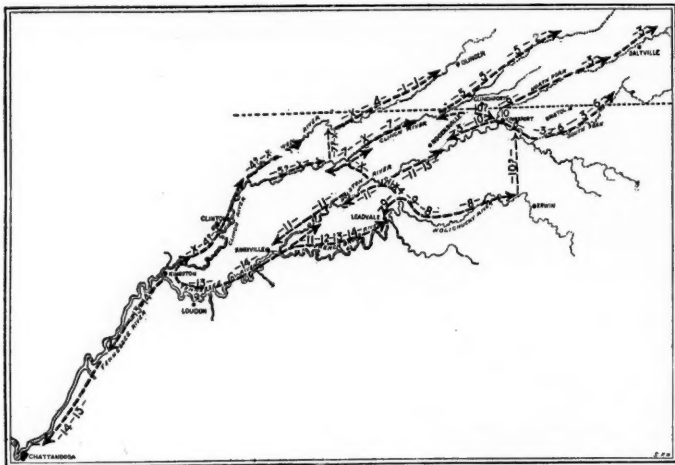

FIG. 3. Map showing the hypothetical migrations of the snails of the genus *Io* in the upper Tennessee River system, as influenced by drainage changes. The numbers refer to the kind of shell illustrated in Fig. 5.

ical evidences and causes of evolution gives much thought, and it is to the present evidences of these changes to which the field ecologist gives much attention.

In my study of migrations of the fresh-water snail *Io,* in the drainage of the upper Tennessee River system (Adams, '15*b*), it was found that there were great cycles of change in the history of the streams, and that there were probably corresponding migrations of the snails. This is shown if we compare the map of ancient hypothetical drainage, Fig. 1, with that of the present, Fig. 2, and the supposed migration of the snails, Fig. 3, and compare these with the map of their present distribution,

Fig. 4. The shells of these snails are shown in Fig. 5. The presence of these snails in the headwaters of streams appears to be due to the ordinary creeping movements of the snails taken in connection with the up-stream migration or growth of the stream habitat, because, on the other hand, the current tends only to favor a down-stream dispersal. Such animals, therefore, appear to be led about *by the migration of their habitat.* This sort of migration is comparable to those land migrations which
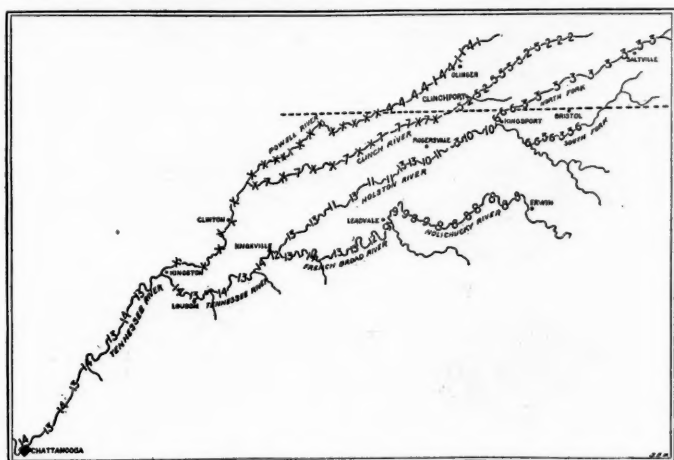

FIG. 4. Map showing the present distribution of the forms of the snail *Io* in the upper Tennessee River system. The numbers refer to the kind of shell illustrated in Fig. 5.

have clearly taken place during climatic migrations, as during the ice age, and during similar changes in humidity, and with base-leveling changes (Woodworth, '94; Adams, '01).

The competition among different kinds of animals has long been recognized as an important factor in animal migrations. Overcrowding produces a condition of stress, and as a result of this stimulus, animals tend to migrate and become diffused from the region of pressure in all possible directions. Thus new conditions are encountered which necessitate changes on the part of the animal, and thus this process continues indefinitely.
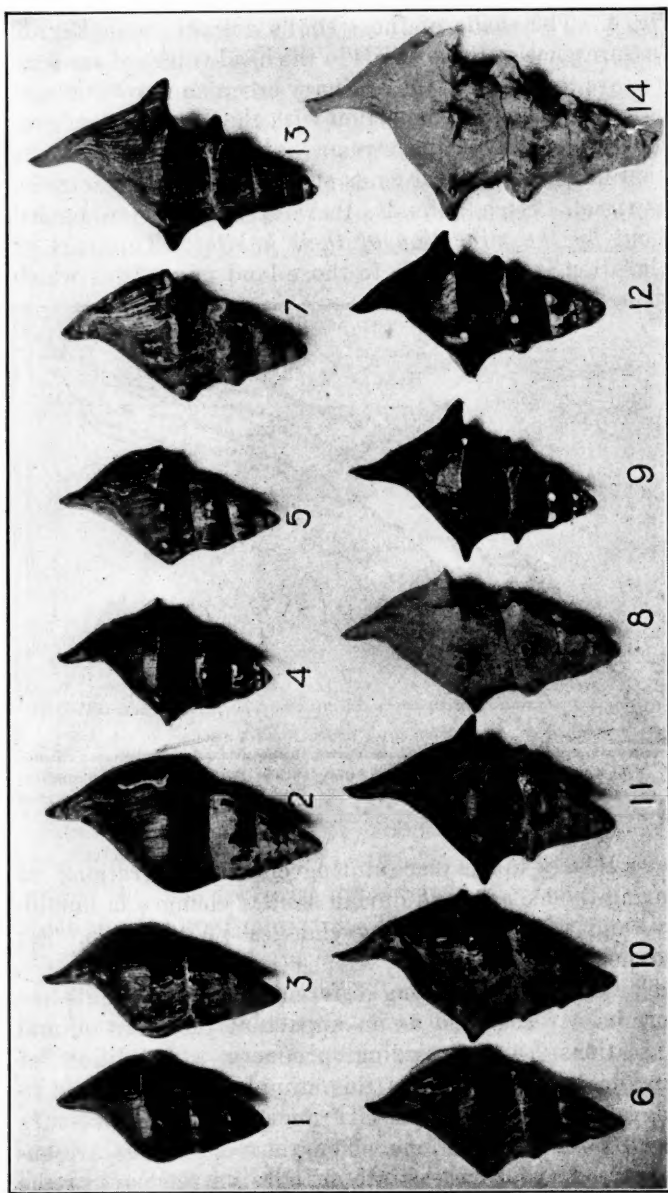
Fig. 5. Illustrations of the main forms of shells in the genus *Io*, whose hypothetical migrations are indicated in Fig. 3.

IV. Summary and Conclusions

The animal should be looked upon as a *dynamic system* which tends to continue in its course of action until changed from within or until diverted by external interference with its system, and until a condition of relative equilibrium is developed by balancing all influences. The behavior of animals should be viewed as a *process* of rhythmical activity.

The *cycle of activity* of the animal agent is a unit of fundamental importance. To study cycles, their *dynamic status,* their degree of relative equilibrium must be determined. In this manner the conditions of stress, the processes of adjustment to strain, and the conditions of relative equilibrium may be recognized and determined. These determinations should be applied to all cycles of activity, that of the life history, and all others. The use of these ideas enables one to apply Bancroft's law—that a system tends to change to minimize external disturbance—to animal activities, and thus one is enabled to explain a large number of diverse observations. Supplementary to Bancroft's law are the influences which tend to accelerate or reinforce, without other change, the condition of the animal.

The *activities of animals* cause them to collide with their environment. Conditions under which animals have become accustomed or attuned are those of relative equilibrium. With departure from these conditions, the animals are stimulated, their system is interfered with, and the animal tends to change until the interference is minimized. The hindrance thus placed upon animal activities are its "limiting factors," and these are to be viewed according to Bancroft's law. This law is not limited to the actions of the individual animal, but includes also the race, and those of animal associations. The Vernon-DeVries law of the *diminishing influence of the environment progressively during ontogeny,* is an example of limiting factors according to Bancroft's law. This law of Vernon's is of great value in the study of

migration in relation to evolution because it suggests the *critical period* at which the stress of the new environment may have its *greatest direct influence upon the new generation* and thus influence its heredity.

The next important category above the animal system is the *law of interacting systems.* The main models of interacting systems are:

1. The physical model of interacting forces, recalling in this connection the law of *inertia,* the tendency of a body to continue in its present state at rest, or in motion, and the law of reinforcement or acceleration.

2. Bancroft's law is that a system tends to change in such manner as to minimize external disturbance. This should be applied to the interaction of all systems. This is a law concerned with responses to stress and to the process of adjustment, and it shows development or evolution of *equilibria.*

3. The phase rule applies to the *result* of responding to stress or *equilibria.* This is thus complementary to Bancroft's law; one is concerned with the condition of stress, and the other with the condition of equilibria.

These laws appear to be universal and not limited solely to the non-living. Irritability may not be causally explained, but *it seems to obey these general laws in the same manner as causal changes.* Applying these laws to animal migration, we see that the present geological age is one of physical stress, and that the process of adjustment to strain is now in operation. The physical stress applies to the air, water, earth and to their interactions. This is an age of physical diversity—tending toward one of simplicity and uniformity. With diversity there are many local cycles of activity in all features of the environment. These cycles of circulation influence the *transportation* of animals, and their active *migrations.* By transportation and migration animals encounter new conditions, new stresses, and change to minimize the disturbance and acclimate themselves to the limit of their

possibilities; and they repeat this cycle with unending monotony and persistence.

December 15, 1917.

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Although these books by Spencer are in many ways not representative of the more recent conceptions, yet strange as it may seem to some, I have seen no better general discussion of biological problems which uses so many thoroughgoing dynamic conceptions.   After familiarity with more modern views, these books may be read with great profit, particularly his discussions of cycles, relative equilibria, and his general conception of life processes.   See footnote on page 488.   Bancroft and Child make no reference to Spencer.   Cf. Höffding, Darwin and Modern Science, 1910, pp. 450–455.

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ERRATA

P. 471, line 23 from top, third word should read ''the.''
P. 472, line 5, for ''ontology,'' read ''ontogeny.''
P. 482, line 29, for ''really,'' read ''readily.''

SOME STUDIES IN BLOSSOM COLOR INHERI-
TANCE IN TOBACCO, WITH SPECIAL REFER-
ENCE TO N. SYLVESTRIS AND N. TABACUM

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THE blossoms of varieties of *Nicotiana tabacum* exhibit three distinct colors, white, carmine and pink.[1]

In the writer's crossing experiments, two white-flowered nicotianas were used, *N. sylvestris,* a species with long, slender, pure white blossoms, and a variety of *N. tabacum* from Honduras (S. P. I. No. 30887), with rather small, pure white blossoms of the *tabacum* type. The pink-flowered variety generally used was the Connecticut Broadleaf variety, although the varieties 70-leaf Cuban, a mammoth type of Cuban which appeared as a mutation in Connecticut in 1912, and Maryland Mammoth also were used. The carmine-blossomed tobacco[2] is a variety of *tabacum* sold by various seedsmen for ornamental purposes under the name giant red-flowering tobacco. This variety breeds true to blossom color and crosses readily with all the commercial varieties of *tabacum*.

CROSSES OF PINK-FLOWERED VARIETIES WITH CARMINE-FLOWERED VARIETIES

In the crosses Pink ♀ × Carmine ♂ and their reciprocals, Carmine, without exception, has been perfectly

[1] The colors carmine and pink have been compared with Ridgway's Color Standards and Color Nomenclature, 1912 edition. The carmine is practically identical with Ridgway's carmine, shown on Plate 1. The pink matches almost exactly his Hellebore Red, shown on Plate 38.

[2] There seems to be little definite information at hand concerning the origin of the carmine-flowered varieties of *N. tabacum*. O. Comes, in his monograph "Delle Razze Dei Tabacchi," *Atti. Del R'Inst. d'Incoraggiamento di Napoli,* Serie 6, 1905, pp. 77-306, speaks of the Nepal tobacco, a variety of *N. tabacum,* as having intensely red blossoms. The Rano variety is also said to have distinctly red blossoms.

dominant, so that all the blossoms of first generation plants bear carmine flowers.

TABLE I

FIRST GENERATION PLANTS OF CROSS CARMINE × PINK

Year	Row	Cross	No. of Plants	Remarks
1915	26A	Carmine ♀ × Pink (Md. Mammoth) ♂......	21	All carmine
1916	21C	Pink (70 leaf Cuban) ♀ × Carmine ♂......	27	" "
1916	26A	Carmine ♀ × Pink (70 leaf Cuban) ♂......	22	" "
1916	35A	Pink (Conn. Broadleaf) ♀ × Carmine ♂....	26	" "
1917	114A	Pink (Conn. Broadleaf) ♀ × Carmine ♂....	50	" "
Total...			146	All carmine

TABLE II

SECOND GENERATION PLANTS OF CROSS CARMINE × PINK

Year	Row	Cross	No. of Plants	Red	Pink
1915	27B	Carmine ♀ × Pink (Md. Mammoth) ♂...	15	13	2
1916	19B	Pink (Conn. Broadleaf) ♀ × Carmine ♂...	39	30	9
1917	90B	Pink (Conn. Broadleaf) ♀ × Carmine ♂...	10	6	4
1917	91B	Pink (Conn. Broadleaf) ♀ × Carmine ♂...	42	29	13
1917	107C	Pink (Conn. Broadleaf) ♀ × Carmine ♂...	23	19	4
1917		Pink (Conn. Broadleaf) ♀ × Carmine ♂...	153	114	39
Total...			282	211	71

From the data shown in Tables I and II, it is evident that the characters pink and carmine behave as typical unit characters, with carmine completely dominant. Segregation takes place in the 2d generation into carmine and pink blossomed plants very close to the theoretical ratio of 3 to 1.

A heterozygous plant of the first generation of the cross Pink (Conn. Broadleaf) ♀ × Carmine ♂ was then crossed with homozygous carmine. Of 115 plants obtained in this cross, all were carmine in color, which is in accord with the expected result.

Heterozygous plants of the first generation were now crossed with recessive pink with the following results.

From these results it is evident that the theoretical ratio 1 : 1 which obtains in such a cross is very closely approached.

TABLE III

CROSSES BETWEEN HETEROZYGOUS PLANTS OF THE FIRST GENERATION OF
THE CROSS (PINK ♀ × CARMINE ♂) AND PINK

Year.	Row.	Cross.	No. of Plants	Red	Pink
1915	18A	A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ × Carmine ♂] ♀ × Pink (White Burley Mammoth) ♂	19	7	12
1915	22	A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ × Carmine ♂] ♀ × Pink (White Burley Mammoth) ♂	41	17	24
1915	26B	A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ × Carmine ♂] ♀ × Pink (Md. Mammoth) ♂	19	11	8
1915	28B	A first generation plant of the cross [Pink (Conn. Broadleaf) ♀ ×Carmine ♂] ♀ × Pink (White Burley Mammoth) ♂	16	7	9
1917		A first generation plant of the cross [Pink (Conn. Broadleaf) ♀× Carmine ♂] ♀ × Pink (White Burley Mammoth) ♂	197	91	106
1917		A first generation plant of the cross [Pink (Conn. Broadleaf) ♀× Carmine ♂] ♀ × Pink (Conn. Broadleaf) ♂	249	130	119
Total..		....	541	263	278

In further studies of the cross Carmine × Pink, the progenies of many extracted, recessive pink-flowered plants of the second generation have been grown, and all have produced pink-flowered lines. Of the carmine-flowered plants of the second generation, some (the heterozygous) have again broken up into Carmine and Pink, while others (homozygous) have given pure Carmine lines.

CROSSES INVOLVING CARMINE OF PINK WITH WHITE

In crosses involving Carmine or Pink with White, white has behaved as a recessive, whether the cross has been made with the white-flowered species *N. sylvestris,* or with the white-flowered variety of *N. tabacum* S. P. I. No. 30887 from Honduras. Carmine, however, is not perfectly dominant in these crosses for plants of the first generation are somewhat lighter red than the carmine itself. In the cross Pink × White (*N. sylvestris*) the blossoms of the first generation are somewhat paler than the usual pink of the tabacum varieties. In crosses

between pink-flowered varieties of *N. tabacum* and White (S. P. I. No. 30887 from Honduras) white has behaved as a recessive. The intensity of the dominant pink depends upon the pink variety used. In some crosses, the blossoms of the first generation plants are similar in color to the pink of the pink parent. In other crosses, the pink of the first generation plants may be noticeably deeper than that of the pink-flowered parent.

A number of heterozygous plants of the first generation of the cross Pink (Conn. Broadleaf) ♀ × Carmine ♂ have been used as mother plants and crossed with the recessive white *N. sylvestris*, with the following results:

42 plants, of which 25 were carmine blossomed and 17 pink blossomed.
41 plants, of which 23 were carmine blossomed and 18 pink blossomed.

Here we have a total of 83 plants, of which 48 possessed Carmine blossoms and 35 possessed Pink blossoms, showing an approximation to the 1:1 ratio. In crosses involving the species *N. sylvestris*, some difficulties are involved, since the first generation plants are usually sterile or nearly so. However, this sterility has been overcome in the cross in which a first generation plant of the cross (Pink (Conn. Broadleaf) ♀ × Carmine ♂) was pollinated with the pollen of *N. sylvestris*. In the second generation of this cross, whites, pinks and carmines appeared. A number of carmine plants were selected and their progenies studied. One known as no. 12, proved to be homozygous for carmine and has bred true to this color for several generations. A sister plant no. 9 with carmine blossoms proved to be heterozygous. In a progeny of 32 plants obtained from this plant, 26 were carmine and 6 were pink blossomed, approximating the theoretical ratio 3:1.

In the cross Carmine × White, using the white-flowered variety of *N. tabacum* S. P. I. No. 30887 from Honduras, the plants produce an abundance of fertile seed. As has been stated, carmine is dominant over white, but it is not

a perfect dominance as in the cross Carmine × Pink, for the blossoms of the first generation plants are somewhat paler than pure carmine. In the second generation there is a segregation into whites, and various degrees of pinks and reds, ranging from light pink to pure carmine. Of 278 second generation plants of this cross, grown in 1917, the blossom colors were grouped as follows:

White	65
Dark pink	26
Light pink	38
Lighter than carmine	95
Carmine	54
Total	278

It is evident that the recessive whites which were easily determined approximated very closely the theoretical 25 per cent. Owing, however, to the uncertainty of analyzing correctly the varied pinks and reds, the carmines which probably represent the homozygous dominants are somewhat below the theoretical 25 per cent. It is quite probable that this class is somewhat smaller than it should be, owing to the difficulty of distinguishing with certainty all the homozygous carmines from the heterozygous somewhat paler carmines.

A number of extracted, recessive whites of the second generation of this cross have been grown and all have produced white-blossomed progenies. These white-blossomed plants have proved somewhat puzzling, however, for some seemed to reveal a hint of color, like an almost imperceptible sheen, that could be detected only in certain lights. So fugacious was this suggestion of color, that I felt inclined to ascribe it to the imagination, until certain crosses were made with pink-flowered varieties as follows:

From the cross Pink (Maryland Mammoth) ♀ × White (extracted) ♂, 54 first generation plants were obtained, of which 17 were carmine, 18 were pink as in the Mammoth, and 19 somewhat lighter than carmine.

In the reciprocal of this cross, *i. e.*, White (extracted) ♀ × Pink (Md. Mammoth) ♂, 43 plants were obtained, of

which 20 were carmine, and 23 were pink blossomed as in the Mammoth.

This same extracted white-flowered plant was also crossed with Pink (Conn. Broadleaf) as follows:

From the cross Pink (Conn. Broadleaf) ♀ × White (extracted) ♂, 51 first generation plants were obtained, of which 12 were carmine or approaching it, and 39 were pink approximating the pink of the Broadleaf parent. It is apparent that the extracted white used in these crosses has somehow retained the factor of Carmine which reappeared in the cross with Pink.

From the results reported in this paper, the Mendelian behavior of the cross Carmine × Pink is particularly striking, and for those who wish to demonstrate before students interested in questions of heredity simple Mendelian behavior in a monohybrid, this particular tobacco cross is especially suitable. Not only is the technique of crossing easy, but a single fertile capsule from a cross will produce several thousand seed. Furthermore, tobacco plants may be readily grown to the flowering stage, in five or six inch pots under greenhouse conditions.

Summary

Among the varieties of tabacum, carmine and pink in crosses behave as unit characters, carmine being dominant. In the second generation perfect Mendelian segregation follows, approximating very closely the theoretical ratio of three carmines to one pink. The extracted recessive pinks and the homozygous carmines breed true. The heterozygous carmines again break up into carmine and pink. If a heterozygous plant of the first generation is crossed with a pure carmine, the progeny will all produce carmine blossoms. If it is crossed with a pink, carmines and pinks will appear in the progeny, approximating the ratio 1 to 1.

In crosses involving carmine or pink with white, white behaves as a recessive, appearing in the second generation.

SHORTER ARTICLES AND DISCUSSION

A BIOLOGICAL SURVEY OF DESCRIBED CERCARIÆ IN THE UNITED STATES*

Among the earlier American zoologists Joseph Leidy alone was a student of cercariæ. From his time to very recent years American cercariæ have received little attention. This may have been due to the greater demands made by other groups of animals, or possibly to the minute size of the larvæ and a failure to appreciate the exact differences of their structure. It could not have been due to a lack of knowledge of the presence of cercariæ, for the European records were abundant and the classical studies of Leuckart, Ercolani and Looss had demonstrated the life-history relations of cercariæ and adult flukes. Moreover, the large number of adult trematode records showed that the larvæ must be fairly abundant.

Within the past few years a revival of study in this larval group has revealed a large number of forms, so that now there are some sixty named species. Only eight of these have dates prior to 1914. The majority of described cercariæ have been worked over by Cort, Faust and O'Roke.

A study of the descriptions of earlier named species shows them to be very general, so that they apply not to the species at all but to larger groups, genera or perhaps even subfamilies. For example, the record of a monostome with three eye-spots instead of characterizing a species merely distinguishes the trioculate from the binoculate group of species. A parallel is found in the diplostomulum commonly known as *Diplostomum cuticula* von Nordmann 1832, which has been recorded from a variety of vertebrate hosts and from equally variable habitats. There is great probability of the existence of several new species concealed beneath these generalized data. Such cases illustrate the futility of generalized descriptions.

Cort emphasizes the value of the excretory system of the cercaria as a basis of description. The conservatism of the system is urged as a basis on which fundamental group relationships of the trematodes can be discovered. Advantage in using this

TABLE I

RECORD OF DESCRIBED CERCARLE IN THE UNITED STATES

Name	Host	Locality and Date	Per Cent. Infection
Monostomes			
1. *C. urbanensis* Cort, 1914	*Physa gyrina* Say	Urbana, Ill., 1913	5.0
2. *C. konadensis* Faust, 1917	*Lymnaea proxima* Lea	Corvallis, Mont., 1916	31.3
3. *C. pellucida* Faust, 1917	*Physa gyrina* Say	Ft. Missoula, Mont., 1916	5.5
4. *C. pellucida* Faust, 1917	*Lymnaea proxima* Lea	Corvallis, Mont., 1916	31.3
5. *C. robusta* Faust, 1918	*Physa gyrina* Say	DeKalb, Ill., 1916	60.0
6. *C. aurita* Faust, 1918	*Goniobasis pulchella* (Anthony)	Homer, Ill., 1917	8.3
7. *C. hyalocauda* Haldeman, 1842	*Physa heterostropha* (Say)	Philadelphia, Pa., 1842 ?	?
8. *C. hyalocauda* Haldeman, 1842	"	Philadelphia, Pa., 1880	?
9. *C. lucania* Leidy, 1877	*Planorbis parvus* Say	Philadelphia, Pa., 1877 ?	Heavy
Amphistomes			
10. *C. inhabilis* Cort, 1914	*Planorbis trivolvis* Say	Lawrence, Kan., 1913	11.1
11. *C. inhabilis* Cort, 1914	" "	Urbana, Ill., 1913	Few
12. *C. inhabilis* Cort, 1914	" "	Lawrence, Kan., 1915	4.5
13. *C. diastropha* Cort, 1914	" "	Chicago, Ill., 1913	5.0
14. *C. diastropha* Cort, 1914	" "	Lawrence, Kan., 1915	4.0
15. *C. cortii* O'Roke, 1917	" "	Cherryvale, Kan., 1915	4.0
16. *C. gorgonocephala* Ward, 1916	Free in plankton, host unknown	Put-in-Bay, O., 1901	Single specimen
Distomes			
17. *C. megalura* Cort, 1914	*Pleurocerca elevatum* Say	Sangamon River, Ill., 1913	1.4
18. *C. megalura* Cort, 1914	*Goniobasis virginica* Say	Princeton, N. J., 1908	?
19. *C. gracilescens* Faust pro *C. gracilis* O'Roke, 1917, preocc			
20. *C. magnacauda* O'Roke, 1917	*Physa integra* Hald.	Chanute, Kan., 1915	4.0
	Planorbis trivolvis Say	Lawrence, Kan., 1915	5.0
21. *C. agilis* Leidy, 1858	"In company with *Planorbis*, *Paludina*, and *Lymnaea*"	Delaware, R., ?	?
22. *C. ascoidea* Leidy, 1877	*Planorbis parvus* Say	Philadelphia, Pa., 1877 ?	Heavy
23. *C. ascoidea* Leidy, 1877	*Lymnaea elodes* Say	Philadelphia, Pa., 1877 ?	?
24. *C. trigonura* Cort, 1914	*Campeloma decisum* (Say)	Hartford, Conn., 1913	11.0
25. *C. wrightii* Ward, 1916	In aquarium, host unknown	Toronto, Can., 1885	Single specimen

TABLE I—Continued

Name	Host	Locality and Date	Per Cent. Infection
Distomes			
26. C. anchoroides Ward, 1916[1]	Free-swimming, host unknown	Lake St. Clair, 1894	—
27. C. douthitti Cort, 1914...........	Lymnaea reflexa Say	Chicago, Ill., 1913	10.3
28. C. douthitti Cort, 1914...........	Lymnaea stagnalis appressa Say	Douglas Lake, Mich., 1915–1916	?
29. C. douthitti Cort, 1914...........	Lymnaea stagnalis perampla Walker	Douglas Lake, Mich., 1915–1916	?
30. C. gracillima Faust, 1917...........	Physa gyrina Say	Bitter Root River, Mont., 1916	19.4
31. C. gracillima Faust, 1917...........	Lymnaea prozima Lea	Missoula, Mont., 1916	3.1
32. C. tuberistoma Faust, 1917...........	Physa gyrina Say	Corvallis, Mont., 1916	5.3
33. C. gigas Faust, 1918...........	Planorbis trivolvis Say	DeKalb, Ill., 1917	56.0
34. C. gigas Faust, 1918...........	" "	Urbana, Ill., 1917	100.0
35. C. gigas Faust, 1918...........	Physa gyrina Say	Pine Creek, Ill., 1917	23.0
36. C. minima pro C. minor Faust, 1918 preoc...	" "	DeKalb, Ill. 1917	6.0
37. C. inversa O'Roke, 1917...........	" "	Lawrence, Kan. 1915	2.0
38. C. echinocauda O'Roke, 1917...........	" "	Lakeview, Kan. 1915	6.0
39. C. quieta O'Roke, 1917...........	Planorbis trivolvis Say	Lawrence, Kan. 1915	15.4
40. C. elephantis Cort, 1918...........	" "	Douglas Lake, Mich., 1914–1916	?
41. C. emarginata Cort, 1918...........	Lymnaea emarginata angulata Sowerby	Douglas Lake, Mich., 1914–1916	?
42. C. douglasi Cort, 1918...........	Physa ancillaria Say	Douglas Lake, Mich., 1914–1916	?
43. C. tardigrada Leidy, 1858...........	Anodonta (fluviatilis) cataracta Say	Philadelphia, Pa. ? ?	?
44. C. tardigrada Leidy, 1858...........	Anodonta (lacustris) marginata Say	Philadelphia, Pa. ? ?	?
45. Cercariaeum helicis Leidy, 1847	Helix albolabris Say	Philadelphia, Pa. ? ?	?
46. C. helicis Leidy, 1847[2]...........	Helix alternata Say	Philadelphia, Pa. ? ?	?
47. C. leptacantha Cort, 1914...........	Campeloma decisum Say	Hartford, Conn., 1913	8.3
48. C. caryi Cort, 1914	Goniobasis virginica Say	Princeton, N. J., 1909	?
49. C. brevicaca Cort, 1914...........	Physa anatina Lea	Manhattan, Kan., 1913	3.2
50. C. crenata Faust, 1917...........	Lymnaea prozima Lea	Ft. Missoula, Mont., 1916	13.6
51. C. isocotylea Cort, 1914...........	Planorbis trivolvis Say	Urbana, Ill., 1914	18.0
52. C. isocotylea Cort, 1914...........	" "	Urbana, Ill., 1916–1917	50.0
53. C. isocotylea Cort, 1914...........	" "	DeKalb, Ill., 1917	6.0
54. C. polyadena Cort, 1914...........	Lymnaea reflexa Say	Chicago, Ill., 1913	2.6

TABLE I—Continued

Name	Host	Locality and Date	Per Cent. Infection
Distomes			
55. C. dendritica Faust, 1917 ...	Lymnaea proxima Lea	Ft. Missoula, Mont., 1916	35.7
56. C. dendritica Faust, 1917 ...	" "	Bitter Root River, Mont., 1916	10.3
57. C. glandulosa Faust, 1917 ...	Physa gyrina Say	Corvallis, Mont., 1916	40.0
58. C. diaphana Faust, 1917 ...	Lymnaea proxima Lea	Corvallis, Mont., 1916	31.3
59. C. micropharynx Faust, 1917	" "	Missoula, Mont., 1916	56.3
60. C. racemosa Faust, 1917 ...	" "	Ft. Missoula, Mont., 1916	10.3
61. C. hemilophura Cort, 1914 ...	Physa gyrina Say	Rockford, Ill., 1913	5.0
62. C. stilifera Faust, 1918 ...	" "	Pine Creek, Ill., 1917	6.6
63. C. haskelli O'Roke, 1917 ...	" "	Lawrence, Kan., 1915	3.0
64. C. greparia O'Roke, 1917 ...	Planorbis trivolvis Say	Cherryvale, Kan., 1915	21.7
65. C. kansiensis O'Roke, 1917 ...	" "	Pratt, Kan., 1915	75.0
66. C. lissorchis fairporti Magath, 1918.	" "	Fairport, Iowa, 1917	10.0
67. C. platyura Leidy, 1890 ...	Lymnaea sp.?	Fort Bridger, Wyo. ?	Free in pool
68. C. reflexa Cort, 1914 ...	Lymnaea reflexa Say	Chicago, Ill., 1913	21.0
69. C. rubra Cort, 1914[a] ...	Campeloma decisum (Say)	Hartford, Conn., 1913	16.6
70. C. trivolvis Cort, 1914 ...	Planorbis trivolvis Say	Urbana, Ill., 1913	Few
71. C. trivolvis Cort, 1914 ...	" "	DeKalb, Ill., 1917	23.3
72. C. biflexa Faust, 1917 ...	Physa gyrina Say	Ft. Missoula, Mont., 1916	7.0
73. C. trisolenata Faust, 1917 ...	" "	Ft. Missoula, Mont., 1916	49.1
74. C. trisolenata Faust, 1917 ...	Planorbis trivolvis Say	Ft. Missoula, Mont., 1916	75.0
75. C. chisolenata Faust, 1918 ...	Physa gyrina Say	Pine Creek, Ill., 1917	8.3
76. C. acanthostoma Faust, 1918.	Planorbis trivolvis Say	Urbana, Ill., 1917	100.0
77. C. acanthostoma Faust, 1918.	Physa gyrina Say	Urbana, Ill., 1917	100.0
78. C. fusiformis O'Roke, 1917 ...	" "	Lawrence, Kan., 1915	1.0
Holostomes			
79. C. flabelliformis Faust, 1917 ...	Physa gyrina Say	Corvallis, Mont., 1916	23.3
80. C. (Tetracotyle) typica Diesing, by Leidy, 1890 ...	Galba catascopium (Say)	Philadelphia, Pa. ? ?	?
81. C. sp. by Rettger, 1896 ...	Lymnaea stagnalis (Linn.)	Terre Haute, Ind. ?	?

[1] Recently the writer has described two species closely related to C. anchoroides: C. brookoveri, from Campeloma sp, Cedar Point, Lake Erie, 1912, and C. macrostoma, free in an aquarium, Urbana, Ill, 1917.

[2] Possibly Agamo distomum.

[3] Agamo distomum.

system lies in the fact that it can be studied entirely in the living cercariæ. The writer has used this method with profit, but in addition has worked out a method of staining the genital organs in the preserved larvæ. This method can be utilized when the worker has access only to preserved larvæ. While the excretory system is indeed a conservative system, the genital system is probably more conservative and less likely to change from cercarial to adult stage. It has been found to be remarkably similar in the large, yet variable in minor, details in groups of cercariæ known to be related through other organs or systems. The best description of a cercaria is probably that which includes both the excretory system as worked out in the living animal and the genital cell masses as depicted in carefully preserved and stained material.

A mere superficial description of the worm is a distinct burden on the literature. The cercaria should be carefully studied in minute detail or not at all. It is the nicety of technic and care in observation which have yielded the number of species now known and bids fair to increase the number vastly in the next few years. It is necessary, then, to urge the investigator in this group to use the utmost care in his work, to describe the minute parts of the organs, and to record the complete biological data available that these records may be of use in life-history investigations.

In order to place the more important biological data of described cercariæ in the United States in a convenient form, a table has been prepared to cover the groups, the authors and dates of the naming of the species, the hosts, localities and dates of collections and the per cent. of infection (see Table I). The same data have been collated from the standpoint of the host in Table II.

A study of the described species shows that the great bulk are distome larvæ. Most of these fall into three groups, the stylet, echinostome and forked-tailed cercariæ. The former group bear evidence of relationship to the Plagiorchiidæ; the echinostome cercariæ are known to be larval Echinostomidæ, and the forked-tailed cercariæ are probably larval schistosomes. The life history of only one species in the group has been worked out with certainty, that of *Cercaria Lissorchis fairporti,* with *Planorbis trivolvis* as larval host, a chironomid larva as intermediate host, and *Ictiobus* spp. as definitive hosts. Of the species recorded

TABLE II

RECORD OF MOLLUSK INFECTION WITH CERCARIÆ

Host Species	Total No. Species	Mono-stome	Amphis-tome	Distome	Holo-stome	Distinct Localities
Planorbis trivolvis............	14	0	3	11	0	7
Planorbis parvus............	3	1	0	2	0	1
Campeloma decisum..........	3	0	0	3	0	1
Lymnæa sp.................	1	0	0	1	0	1
Lymnæa proxima............	8	2	0	6	0	1
Lymnæa emarginata angulata..	1	0	0	1	0	1
Lymnæa elodes..............	1	0	0	1	0	1
Lymnæa stagnalis............	1	0	0	0	1	1
Lymnæa stagnalis appressa....	1	0	0	1	0	1
Lymnæa stagnalis perambla ...	1	0	0	1	0	1
Lymnæa reflexa..............	3	0	0	3	0	1
Physa gyrina................	19	3	0	15	1	5
Physa anatina...............	1	0	0	1	0	1
Physa heterostropha..........	1	1	0	0	0	1
Physa integra...............	1	0	0	1	0	1
Physa ancillaria.............	1	0	0	1	0	1
Goniobasis pulchella.........	1	1	0	0	0	1
Goniobasis virginica..........	2	0	0	2	0	1
Pleurocerca elevatum..........	1	0	0	1	0	1
Galba catascopium...........	1	0	0	0	1	1
Helix alternata..............	1	0	0	1	0	1
Helix albolabris..............	1	0	0	1	0	1
Anodonta cataracta..........	1	0	0	1	0	1
Anodonta marginata..........	1	0	0	1	0	1
Free-swimming only.........	3	0	1	2	0	3
Total No. distinct host records	72	8	4	57	3	
In two or more hosts.........	11	2	0	9	0	
Net species.................	61	6	4	48	3	

for the United States only one, *C.* (*Tetracotyle*) *typica* Diesing, 1858, is recorded for another locality than North America.

The larval hosts are without exception mollusks. All except two, *Anodonta cataracta* and *A. marginata,* are Gasteropoda. Several of the species have been found in two snails, although none have been recorded as infecting three or more hosts. Usually where the species occurs in two hosts the infection of the one is more widely spread and heavier than that of the other. Several records show the parasitism of several species of cercariæ within the same host species in the same locality. In fact, the writer found as many as four trematode species within the same host individual (*Planorbis trivolvis*) at DeKalb, Illinois, in August, 1917. The occurrence of two cercariæ species in the same host individual is commonly found in the records. In this case one of the parasites usually has a heavier hold on the host than the other and constitutes the major infection.

Limited geographical areas have been covered in the surveys for cercariæ. Two drainage systems of the Atlantic slope, isolated regions around the Great Lakes, a portion of the upper Columbia and an isolated region in Wyoming, together with more widely investigated areas in the Mississippi basin, constitute the localities in which collections have been made. The entire south, southeast and southwest constitute vast unexplored areas, the former two of which should yield a great number of species. In addition, the variation of species of flukes in snails from one season to another makes it highly probable that many more species occur in the Mollusca of the areas surveyed than the records show. Table I shows that one distome species, *Cercaria megalura,* has been found in *Goniobasis virginica* from the Atlantic slope, and in *Pleurocerca elevatum* from the Mississippi basin; and that *C. inhabilis* and *C. diastropha* have been found on both the eastern and western slopes of the Mississippi drainage. On the other hand, none of the species described for the Bitter Root Valley have been recorded east of the Rocky Mountains.

Records of percentage of infection from larval flukes vary from a few hundredths of a per cent. for certain cercariæ described by Sisnitzin in 1911 from the Black Sea to a heavy infection of every individual of a particular species in a locality. The lowest infection record for the United States is one per cent. (*C. fusiformis* in *Physa gyrina*). On the other hand, several heavy infections have been recorded, including three with total infection. The mollusks most heavily infected are the ubiquitous species, *Planorbis trivolvis* and *Physa gyrina,* and the western species, *Lymnæa proxima.* In the case of the *Planorbis* and the *Lymnæa* the average heavy infection is caused by distome cercariæ. The heavy infection among the physas is caused by monostome and holostome larvæ.

Table II, which summarizes the infection from the host point of view, shows that *Lymnæa proxima* has the greatest number of species per habitat. *Planorbis trivolvis* has been found to be infected in the greatest number of localities, while *Physa gyrina* is the only mollusk to harbor three groups of *Digenea.* Of the sixty named species listed in Tables I and II eleven are recorded from two hosts.

Accompanying the cercariæ in the mollusks are the parthenitæ (sporocysts and rediæ) of these cercariæ. The cercariæ develop parthenogenetically within these parthenitæ. Typically, as in

the life history of *Fasciola hepatica,* the sporocyst and redia generations both occur, but in several groups, notably in the stylet cercariæ and the furcocercariæ the redia stage has been omitted or replaced by another sporocyst stage.

Sporocysts and rediæ have not been sufficiently distinguished. The sporocyst is an adult which has lost its digestive tube, while a redia is an adult which possesses both a rhabdocœle gut and a pharyngeal sphincter. In certain sporocysts the sphincter still remains, as in *C. dendritica.* In other sporocysts, as in some furcocercariæ, while no definitely differentiated sphincter is present, the anterior end of the sac is muscular, turning in and out like the finger of a glove. This may easily be mistaken for a rhabdocœle gut.

The cercariæ develop within the parthenitæ and usually at the time of maturity break out of the parent and work their way through the tissues of the host into the water. In case no suitable host is at hand in which the larvæ may continue development they ordinarily encyst. Groups like the furcocercariæ, however, are not known to encyst. On the other hand, the writer has found encysted larvæ of *C. biflexa* within the larval host and encysted larvæ of *C. micropharynx* even within the parent sporocysts.

The parthenitæ of monostome, amphistome and holostome cercariæ are rediæ. Parthenitæ of certain groups of distome cercariæ are sporocysts and of other groups of distome cercariæ are rediæ, although some of the records are conflicting. This shows the need of the accurate determination of the parthenita of each cercaria, since the parthenita is a distinct generation in the life history of the species.

In order that the records may not be confusing the writer proposes the name *Cercaria gracilescens* for *C. gracilis* O'Roke 1917, preoccupied by La Valette 1855, and *C. minima* for *C. minor* Faust 1918, preoccupied by Lebour 1912.

In conclusion, the effect of the larva on the mollusk must be emphasized. It is an observable fact that heavily infected snails die sooner than uninfected ones. The cause of this mortality is both the mechanical disruption of the tissues of the infected mollusk and the pathological changes within the cells of the infected animal. A pathologico-chemical study of this relationship would be of great value to parasitologist and malacologist alike.   ERNEST CARROLL FAUST

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ON REGENERATION AND THE RE–FORMATION OF LUNULES IN MELLITA[1]

THE ambulacral lunules of the genus *Mellita* are characteristically developed by the inclusion of reëntrant marginal notches; except that in *M. sexiesperforata* these lunules, like the interambulacral lunule in this and in related genera, is formed by resorption through the test.[2] In a few species the ambulacral lunules are permanently maintained as open marginal notches, and Jackson[3] has called attention to the fact that in *Encope annectans* Jackson, the adult interambulacral lunule is represented by mere dorsal and ventral furrows, not sufficiently deep to meet and form a hole through the test. In view of the possibly exceptional character of the formation of the ambulacral lunules in *M. sexiesperforata,* note may be made of the manner in which the lunules of this species are re-formed during regenerative changes consequent upon natural injury. For in collections of *Mellita* comprising half-a-dozen or more individuals of adult size it is rarely found that every specimen presents a complete and regular marginal outline. The degree of irregularity is in most instances not large, but in some cases amounts, at the deepest point, to a radial deficiency of 13 mm. in a specimen 12 cm. in transverse diameter. I have found no irregularities of this character in specimens less than 8 cm. in transverse diameter. The nature of these deficiencies is such as to suggest that they have been inflicted by other bottom-feeding animals, possibly fishes. The wound-surfaces seem, however, to be readily covered over; and the various degrees of alteration toward a more perfect outline, exhibited in different specimens, show that relatively complete restitution is possible.

It is a noteworthy fact that these injuries are almost entirely confined to that end of the animal which is morphologically the posterior (cf. Figs. 1, 2, 3). It seems to me possible that this fact may be understood upon the assumption that when burrowing the anatomically anterior end of the "sea plate," which is somewhat more sharply pointed than the posterior, is the one

[1] Contributions from the Bermuda Biological Station for Research.

[2] Agassiz, A., "Revision of the Echini," pp. 320–324. Clark, H. L., 1904, "Echinoderms of the Woods Hole Region," *Bull. U. S. Bur. Fish.* for 1902, pp. 545–576 (p. 565).

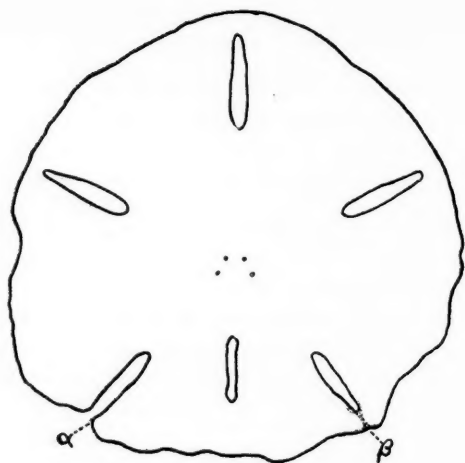[3] Jackson, R. T., 1917, *Proc. U. S. Nat. Mus.,* Vol. 53, pp. 489–501 (p. 494).

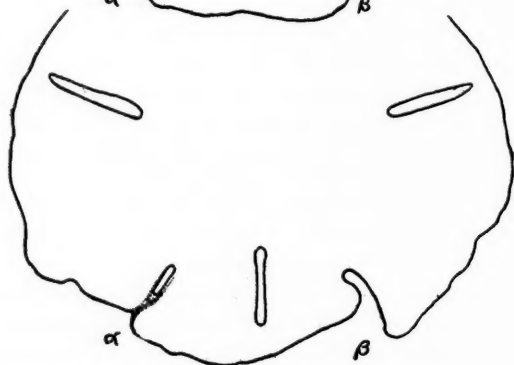FIG. 1. Outline of a *Mellita sexiesperforata* showing at α and at β two stages
in the re-formation of a posterior lunule. At β a furrow, deeper on the ventral
surface, marks the region of union of the material from the two interambulacra.
(× 1.) From life.

FIG. 2. Another case, showing lunules 1 and 5 in process of being closed.
(× 1.) From living animals.

FIG. 3. At α the concrescence of the old lunule-walls has been carried to an
extent such that the distance between the distal end of the lunule and the mar-
gin of the disc is actually greater than in the case of a lunule normally formed.
Here also the furrow indicated by shading is deeper on the ventral surface. At
β, deformation of a lunule through growth after injury. (× 1.) From life.

which is carried ahead.[4]   These animals do burrow beneath the surface of the sand when the weather is at all stormy, and, if this assumption be valid, the posterior end might then be exposed (or even separated somewhat from the bottom) to a greater extent than at other times. If the process of emergence from the sand is somewhat different from, or quicker than, that involved in burrowing, one could understand why the anterior end is rarely, if ever, damaged, as might otherwise be expected if differential exposure of some kind alone determines the incidence of injuries; there are, of course, other possibilities.

However they originate, the restorative phenomena which these posterior injuries entail show that the ambulacral lunules of *M. sexiesperforata* May, in regeneration, follow a method of formation resembling, in a measure, that adhered to in the normal development of these lunules by other mellitas. The individuals herewith depicted in outline (Figs. 1, 2, 3) exhibit several stages in a process of lunule-completion through the concrescence of the growing edges of the disc. It is difficult to decide whether this process is of a specific regulatory character, ''aiming at'' the reconstitution of the lunules, or whether it represents merely the inevitable consequence of ordinary (though accelerated) growth at the margin of the mellita disc, and is, perhaps, for this reason, devoid of any recapitulatory significance. An inspection of Fig. 1 will show that at α there is evident a decided out-bulging of the disk-margin, at the point of union with the old outline of the lunule. This out-bulging, seen also at β in Fig. 2, and at β in Fig. 3, shows definite growth of the tissue toward the opposite lunule-wall in interambulacrum V. At β in Fig. 1 an outgrowth of this type has met and fused with a less extensive outgrowth from the opposite lunule-boundary; here, as at α in Fig. 2, it will be noted that the lateral extension of interambulacral area V is not confined merely to the margin of the disc, but affects also the whole lateral wall of the lunule on that side,—provided the injury be sufficiently extensive—so that closure of the lunule is slow. If the original disturbance be small, as at β in Fig. 1, this and other similar cases show that reparation may be relatively complete. On the other hand, more extensive injury, as at β in Fig. 3, seems to result in ''regeneration'' which is not so quickly effective as, for example, in β, Fig. 1; under these circumstances the posterior extension of the substance of interambulacrum I,

[4] Cf. Cole, L. J., 1913, *Jour. Exp. Zool.*, Vol. 14, pp. 1–32.

not met by growth from interambulacrum V, produces a relatively considerable distortion of the old lunule. Moreover, the coalescence of the lunule-walls may be carried to a length which seems greater than it need be, as a α in Fig. 3. For these reasons the idea of a specific regulatory character in the re-formation of the lunule seems unnecessary.

It would be of interest to observe the effect, upon the course of regeneration, of an injury deep enough to remove the area of a lunule down to its proximal border; I have seen no cases of this kind, nor any in which the interambulacral lunule had been affected.

Morgan[5] was unable to find in the literature any mention of regeneration among echini. The present observations may consequently help to fill a gap at that point, since I am not aware that any one has previously commented upon the matter, although the conditions described are perhaps well known to other students of echinoderms. For *M. pentapora* cases have indeed been noted in which a lunule, unclosed, extended to the periphery of the disc; but these instances have been referred either to accidental injury or to delayed growth, and "repair" phenomena seem not to have been observed. In *M. sexiesperforata* regeneration (of a sort) does undoubtedly occur, giving evidence of a respectable degree of plasticity in a stony structure where such might not be expected.

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[5] "Regeneration" (1901), p. 105.